Space for WHAM: a multi-region, multi-stock generalization of the Woods Hole Assessment Model with an application to black sea bass

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Main Message

Describes the multi-region, multi-stock generalization of WHAM and its usage to evaluate evidence of alternative hypotheses about temperature effects on recruitment of black sea bass stock components.

Abstract

The Woods Hole Assessment Model (WHAM) is a state-space age-structured assessment model that is used to assess and manage many stocks in the Northeast US. We first describe a multi-stock, multi-region extension of WHAM that treats the population and fleet dynamics seasonally and allows movement by season and region to be functions of time- and age-varying autocorrelated random effects and environmental covariates. We then illustrate the model by applying it to data for the northern and southern components of the NEUS black sea bass stock and evaluate alternative hypotheses of bottom temperature and random effects on recruitment and natural mortality. We show strong evidence for temperature effects on recruitment, primarily for the northern stock component, and no evidence for including random effects or temperature effects on age 1 natural mortality.

Introduction

A state-space statistical approach and maximum marginal likelihood or Bayesian fitting of stock assessment models allows estimation of time- and age-varying population attributes as random effects Miller et al. (2016b). This estimation approach is considered an essential feature of gold-standard assessment models that we use in tactical management of commercially important fish stocks (Punt et al. 2020). The State-space Assessment Model (SAM, Nielsen and Berg 2014) continues to be developed and remains widely used within ICES to assess European fish stocks. Various state-space models are being used to manage cod and plaice stocks in the waters of Eastern Canada (Perreault et al. 2020; Varkey et al. 2022) and to the south, the Woods Hole Assessment Model (WHAM, Stock and Miller 2021) is now used to assess many fish stocks in the Northwest Atlantic Ocean (NEFSC 2022a, 2022b; NEFSC 2024).

WHAM is an R package developed and maintained at NOAA's Northeast Fisheries Science Center (https://timjmiller.github.io/wham, Miller and Stock 2020; Stock and Miller 2021). WHAM can be configured to fit a wide range of age-structured models from traditional statistical catch-at-age models without any random effects to models with several time and age varying process errors and possibly effects of environmental covariates on various demographic parameters. Like SAM, WHAM models are built using the Template Model Builder package (TMB, Kristensen et al. 2016) which provides a computationally efficient means of fitting an extremely wide class of models with random effects. WHAM has undergone active development since its creation and includes random effects options for in recruitment, inter-annual transitions numbers at age (hereafter referred to as "survival"), fishery and index selectivity, natural mortality, and catchability.

However, WHAM has up to now only allowed models with one stock (component) and a single region and without seasonal changes in stock dynamics. Using such models for stocks that have subcomponents with varying seasonal movement can provide incorrect inferences and poor management advice (Ying et al. 2011; Cao et al. 2014; Bosley et al. 2022). Furthermore, the ability to account for spatial structure and model multiple stocks are also important features of leading-edge assessment modeling frameworks (Punt et al. 2020). We describe here the implementation of these features and other extensions since Stock and Miller (2021) in WHAM version 2.0. Many of these new configuration options can be useful whether modeling 1 or more stocks and regions.

This extension of WHAM was developed in concert with a stock assessment for black sea bass through the NEFSC research track assessment process where new modeling frameworks were recently examined and modeling multiple stocks or stock components simultaneously was of interest (NEFSC 2023). [Text on black sea bass here] We apply WHAM 2.0 to two stock components of black sea bass off the coast of the NEUS and evaluate evidence for alternative hypotheses of temporal variation and effects specifically of bottom temperature on recruitment and natural mortality of age 1 individuals.

Methods

WHAM description

Many of the options and equations of WHAM version 2.0 are the same as those in Stock and Miller (2021), so we will only describe extensions and differences that have occurred since their first description of WHAM. The new version of WHAM can model multiple stocks and survival, movement, harvest and natural mortality are tracked for each stock. Much of the description below is for a specific stock s, but, for simplicity, this subscript is implicit except when necessary.

The probability transition matrix

Because individuals may be alive in one of several regions or harvested in one of several fleets, it is helpful to consider these as distinct categories or states and treat the number of individuals occurring in each category over time as a multi-state model. Approaches to modeling transitions among these tates may treat time discretely (e.g., Arnason 1972; Schwarz et al. 1993) or continuously (e.g., Hearn et al. 1987; Commenges 1999; Andersen and Keiding 2002). Multi-state models can define a probability transition matrix (PTM) that describes the probability of individuals occurring in different states at the end of a time interval δ, conditional on being in each of those state at beginning of the interval. For fish populations these states would be defined as being alive in a particular region or being dead due to fishing from a particular fleet or natural mortality. The time interval i with duration δ_i would be a season and the PTMs would be uniquely defined for each stock by season i, year y, and age a on January 1. Each row and column of the PTM correspond to one the states: alive in region r, dead in fleet f, or dead from natural causes. The probabilities in each row sum to unity and assume an individual is in the corresponding state at the beginning of the interval. Given n_R regions and n_F fleets, the square PTM ($n_R + n_F + 1$ rows and columns) as a function of sub-matrices is

$$\mathbf{P}_{y,a,i} = \begin{bmatrix} \mathbf{O}_{y,a,i} & \mathbf{H}_{y,a,i} & \mathbf{D}_{y,a,i} \\ 0 & \mathbf{I}_H & 0 \\ 0 & 0 & 1 \end{bmatrix} \tag{1}$$

where

$$\mathbf{O}_{y,a,i} = \begin{bmatrix} O_{y,a,i}(1,1) & \cdots & O_{y,a,i}(1,n_R) \\ \vdots & \ddots & \vdots \\ O_{y,a,i}(n_R,1) & \cdots & O_{y,a,i}(n_R,n_R) \end{bmatrix}$$

is the $n_R \times n_R$ matrix defining survival and occurring in each region at the end of the interval,

$$\mathbf{H}_{y,a,i} = \begin{bmatrix} H_{y,a,i}(1,1) & \cdots & H_{y,a,i}(1,n_F) \\ \vdots & \ddots & \vdots \\ H_{y,a,i}(n_R,1) & \cdots & H_{y,a,i}(n_R,n_F) \end{bmatrix}$$

is the $n_R \times n_F$ matrix defining probabilities of being captured in each fleet during the interval, and $\mathbf{D}_{y,a,i}$ is the $n_R x 1$ matrix of probabilities of dying due to natural mortality during the interval. We have the identity matrix $\mathbf{I}_H$ for the states for capture by each fleet and a 1 for the state for natural mortality because the probabilities of being in one of the mortality states given starting the interval in that state is unity (no zombies allowed).

WHAM uses these PTMs to model abundance proportions in each state rather than true probabilities where numbers in each state would be multinomial distributed as in a model for tagging data where fates of individual fish are assumed independent. The PTMs determine the expected numbers 1) in each state on January 1 of year $t+1$ at age $a+1$ given the abundances at age a on January 1 of year t, 2) captured over the year in each fleet, 3) available to each index, and 4) alive at the time and in the region where spawning occurs.

Single region PTMs

When there is only one region,

$$\mathbf{P}_{y,a,i} = \begin{bmatrix} S_{y,a,i} & \mathbf{H}_{y,a,i} & D_{y,a,i} \\ 0 & \mathbf{I}_H & 0 \\ 0 & 0 & 1 \end{bmatrix} \tag{2}$$

where $S_{y,a,i} = e^{-Z_{y,a,i}\delta_i}$, $\mathbf{H}_{y,a,i}$ is a 1 x n_F matrix with elements for each fleet f: $\frac{F_{y,a,i,f}}{Z_{y,a,i}}\left(1 - e^{-Z_{y,a,i}\delta_i}\right)$, $D_{y,a,i} = \frac{M_{y,a}}{Z_{y,a,i}}\left(1 - e^{-Z_{y,a,i}\delta_i}\right)$, and $Z_{y,a,i} = M_{y,a} + \sum_{f=1}^{n_F} F_{y,a,i,f}$ is the total mortality rate.

Multi-region PTMs

When there is more than 1 region, WHAM can model survival and movement as processes occurring sequentially or simultaneously. The sequential assumption is used widely in spatially explicit model (e.g., SS3). Under the sequential assumption, survival and death occur over the interval and movement among regions occurs instantly at either the beginning or the end of the interval. WHAM is configured to have movement occur after survival and mortality:

$$\mathbf{O}_{y,a,i} = \mathbf{S}_{y,a,i}\boldsymbol{\mu}_{y,a,i}$$

where $\mathbf{S}_{y,a,i}$ is a $n_R \times n_R$ diagonal matrix of proportions surviving in each region (given they start in that region)

$$\mathbf{S}_{y,a,i} = \begin{bmatrix} e^{-Z_{y,a,i,1}\delta_i} & 0 & \cdots & 0 \\ 0 & e^{-Z_{y,a,i,2}\delta_i} & \cdots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & \cdots & 0 & e^{-Z_{y,a,i,n_R}\delta_i} \end{bmatrix}$$

and $\boldsymbol{\mu}_{y,a,i}$ is a $n_R \times n_R$ matrix of probabilities of moving from one region to another or staying in the region they occurred at the beginning of the interval:

$$\boldsymbol{\mu}_{y,a,i} = \begin{bmatrix} 1 - \sum_{r' \neq 1} \mu_{1 \to r',y,a,i} & \mu_{1 \to 2,y,a,i} & \cdots & \mu_{1 \to R,y,a,i} \\ \mu_{2 \to 1,y,a,i} & 1 - \sum_{r' \neq 2} \mu_{2 \to r',y,a,i} & \cdots & \mu_{2 \to R,y,a,i} \\ \vdots & \vdots & \ddots & \vdots \\ \mu_{R \to 1,y,a,i} & \cdots & \mu_{R \to R-1,y,a,i} & 1 - \sum_{r' \neq R} \mu_{R \to r',y,a,i} \end{bmatrix}$$

WHAM assumes each fleet f can harvest in only 1 region (r_f) during specified seasons. So, for each fleet f, row r_f and column f of $\mathbf{H}_{y,a,i}$ will be $F_{y,a,i,f}\left(1 - e^{-Z_{y,a,i,r}\delta_i}\right)/Z_{y,a,i,r}$ when fleet f is harvesting during the interval δ_i and all other elements will be zero. Row r of the single-column matrix $\mathbf{D}_{y,a,i}$ is $M_{y,a,r}\left(1 - e^{-Z_{y,a,i,r}\delta_i}\right)/Z_{y,a,i,r}$

When survival and movement are assumed to occur simultaneously, all movement and mortality parameters are instantaneous rates. We obtain the probability transition matrix over an interval δ_i by exponentiating the instantaneous rate matrix (Miller and Andersen 2008)

$$\mathbf{P}_{y,a,i} = e^{\mathbf{A}_{y,a,i}\delta_i}$$

The instantaneous rate matrix takes rates of movement between regions and the mortality rates for each fleet and region. Along the diagonal is the negative of the sum of the other rates (the hazard) so each row sums to zero. For two regions and one fleet operating in each region:

$$\mathbf{A}_{y,a,i} = \begin{bmatrix} a_{y,a,i,1} & \mu_{1\to 2,y,a,i} & F_{y,a,i,1} & 0 & M_{y,a,1} \\ \mu_{2\to 1,y,a,i} & a_{y,a,i,2} & 0 & F_{y,a,i,2} & M_{y,a,2} \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}.$$

where $a_{y,a,i,r} = -(\mu_{r\to r',y,a,i} + F_{y,a,i,r_f} + M_{y,a,r})$. When there is one region, n_f fleets, and $\delta_i = 1$, exponentiating the instantaneous rate matrix results in the PTM defined in Eq. 2.

Seasonality

Seasonality can be configured to accommodate characteristics of spawning, movement, and fleet-specific behavior. The annual time step can be divided into K (any number) seasons and the interval size δ_i for each season i need not be equal to any other seasonal interval. Under the Markov assumption, the PTM of surviving and moving and dying over K intervals $\delta_1, \ldots, \delta_K$ (i.e., the entire year) is just the product of the PTMs for each interval:

$$\mathbf{P}_{y,a}(\delta_1, \ldots, \delta_K) = \prod_{i=1}^{K} \mathbf{P}_{y,a,i}(\delta_i).$$

For a stock spawning at some fraction of the year $0 < t_s < 1$ in interval δ_j, the fraction of time in season j is

$$\delta_{s,j} = t_s - \sum_{i=0}^{j-1} \delta_i$$

and the PTM defining the proportions in each state at time t_s for age a is

$$\mathbf{P}_{y,a}\left(\delta_1, \ldots, \delta_{j-1}, \delta_{s,j}\right) = \mathbf{P}_{y,a}\left(t_s\right) = \left[\prod_{i=1}^{j-1} \mathbf{P}_{y,a,i}(\delta_i)\right] \mathbf{P}_{y,a,j}(\delta_{s,j}). \quad (3)$$

Similarly, for an index m occurring at fraction of the year t_m in interval δ_j the proportions in each state at the time of the observation is

$$\mathbf{P}_{y,a}\left(\delta_1, \ldots, \delta_{j-1}, \delta_{m,j}\right) = \mathbf{P}_{y,a}\left(t_m\right) = \left[\prod_{i=1}^{j-1} \mathbf{P}_{y,a,i}(\delta_i)\right] \mathbf{P}_{y,a,j}(\delta_{m,j}). \quad (4)$$

Numbers at age

When there are n_R regions and n_F fleets, The vector of abundance in each state at age $a > 1$ on January 1 is $\mathbf{N}_{y,a} = (\mathbf{N}'_{O,y,a}, \mathbf{0}')'$ where $\mathbf{N}_{O,y,a} = (N_{y,a,1}, \dots, N_{y,a,n_R})'$ is the number in the states corresponding to being alive in each region and $\mathbf{0}$ is a vector $(n_F + 1)$ for the numbers captured in each fleet and dead from natural mortality because no age a fish have died yet on January 1.

Each stock s is assumed to spawn and recruit in one region r_s. So for age $a = 1$, $\mathbf{N}_{O,y,1}$ is 0 except for row $r = r_s$. Options for configuring recruitment $(N_{y,1,r_s})$ for each stock are the same as previous versions of WHAM. If recruitment is assumed to be a function of spawning stock biomass (SSB), it is only the spawning population in region r_s at the time of spawning constitutes the SSB in the stock-recruit function. However, models can configure spawning individuals to occur in other regions at the time of spawning. Aside from treating recruitment as a random walk, the general model for annual recruitment as random effects is

$$\log\left(N_{y,1,r_s}\right) | \mathrm{SSB}_{y-1,r_s} = f\left(\mathrm{SSB}_{y-1,r_s}\right) + \varepsilon_{y,1,r_s}$$

where

$$\mathrm{SSB}_{s,y} = \sum_{a=1}^{A} w_{s,y,a} \mathrm{mat}_{s,y,a} \mathbf{O}_{s,y,a,r_s}(t_s)' \mathbf{N}_{O,s,y,a}$$

where $w_{s,y,a}$ is the mean weight at age of spawning individuals, $\mathrm{mat}_{s,y,a}$ is the maturity at age, and $\mathbf{O}_{s,y,a,r_s}(t_s)$, the r_s column of the upper-left submatrix of Eq. 3, are the probabilities of surviving and occurring in region r_s at time t_s given being alive in each region at the start of the year.

As in previous versions of WHAM, the transitions in numbers at age from one year to another after recruitment can be treated deterministically or as functions of random effects. The predicted numbers at age in year y at age a for a given stock are vector analogs $(\mathbf{N}_{O,y,a})$ of the equations for numbers at age in the standard WHAM model (Stock and Miller 2021). For ages $a = 2, \dots, A-1$, where A is the plus group, the expected number alive in each region at the beginning of the following year and next age class age can be obtained from the first n_R elements of the vector

$$\mathbf{P}'_{y-1,a-1} \mathbf{N}_{y-1,a-1}.$$

The numbers alive in each region can also be modeled more simply using the sub-matrix $\mathbf{O}_{y,a}$. The general model for the transitions in abundance at age is

$$\log\left(\mathbf{N}_{O,y,a}\right)|\mathbf{N}_{O,y-1,a-1} = \log\left(\mathbf{O}'_{y-1,a-1}\mathbf{N}_{O,y-1,a-1}\right) + \boldsymbol{\varepsilon}_{y,a}$$

for ages $a = 2, \ldots, A-1$, and for the plus group

$$\log\left(\mathbf{N}_{O,y,A}\right)|\mathbf{N}_{O,y-1,a-1}, \mathbf{N}_{O,y-1,A} = \log\left(\mathbf{O}'_{y-1,A-1}\mathbf{N}_{O,y-1,A-1} + \mathbf{O}'_{y-1,A}\mathbf{N}_{O,y-1,A}\right) + \boldsymbol{\varepsilon}_{y,A}.$$

When the transitions in abundance at age are treated deterministically, $\boldsymbol{\varepsilon}_{y,a} = 0$. The stock- and region-specific errors $\boldsymbol{\varepsilon}_{y,a}$ are independent, but the same correlation structures as previous versions are possible across ages and years for a given stock and region. When there is autocorrelation with age, WHAM now assumes this applies only to ages $a > 1$ by default so that recruitment random effects are independent of those for for the annual transitions of older age classes. So the general covariance structure for a given stock at ages $a > 1$ in region r is that of a two-dimensional first-order autoregressive (2DAR1) process

$$Cov\left(\epsilon_{y,a,r}, \epsilon_{y',a',r}\right) = \frac{\rho_{N,\text{age},r}^{|a-a'|}\rho_{N,\text{year},r}^{|y-y'|}\sigma_{N,a,r}\sigma_{N,a',r}}{\left(1-\rho_{N,\text{age},r}^2\right)\left(1-\rho_{N,\text{year},r}^2\right)}$$

and that for age 1 is just AR1 across years

$$Cov\left(\epsilon_{y,1}, \epsilon_{y',1}\right) = \frac{\rho_{N,1,\text{year}}^{|y-y'|}\sigma_{N,1}^2}{1-\rho_{N,1,\text{year}}^2}.$$

Since recruitment for a given stock currently only occurs in one region r_s there is only a single time-varying recruitment random effect for each stock.

Initial numbers at age

Initial numbers at age for each stock and region can be treated as age-specific fixed effects or with an equilibrium assumption as in previous versions of WHAM. For the equilibrium option there are two parameters for each stock: the stock-specific fully-selected fishing mortality rate $\log \widetilde{F}$ and the recruitment in year 1 $\log N_{1,1,r_s}$. A stock-specific equilibrium fishing mortality at age by fleet $\tilde{F}_{a,f}$ is the product of $\widetilde{F}$ and the selectivity across fleets in the first year

$$\text{sel}_{1,a,f} = \frac{F_{1,a,f}}{\max_a \sum_{f=1}^{n_F} F_{1,a,f}}.$$

We use $\widetilde{F}_{a,f}$ to define an equilibrium abundance per recruit by region at age a conditional on recruiting to each region

$$\widetilde{\mathbf{O}}_a = \begin{cases} \prod_{j=0}^{a-1} \mathbf{O}_j & 1 \leq a < A \\ \left[\prod_{j=0}^{a-1} \mathbf{O}_j\right] (\mathbf{I} - \mathbf{O}_A)^{-1} & a = A \end{cases} \tag{5}$$

where $\mathbf{O}_j$ is the equilibrium probability of surviving age a and occurring in each region and $\mathbf{O}_0 = \mathbf{I}$. Natural mortality and movement rates in the first year of the model are also used in Eq. 5. For the plus group $a = A$, $(\mathbf{I} - \mathbf{O}_A)^{-1}$ is a "fundamental matrix' ' derived using the matrix version of the geometric series (Kemeny and Snell 1960). Recall that recruitment for stock s only occur in region r_s so, the equilibrium initial numbers at age a by region are

$$\mathbf{N}_{O,1,a} = \widetilde{\mathbf{O}}'_a \mathbf{N}_{O,1,1}.$$

The initial abundances at age can also be treated as independent or as AR1 random effects. Defining the vector of initial abundance at age in region r as $\mathbf{N}_{O,1,r}$, the general model is

$$\log \mathbf{N}_{O,1,r} = \theta_{N_1,r} + \boldsymbol{\varepsilon}_{N_1,r}$$

where

$$Cov\left(\varepsilon_{N_1,a,r}, \varepsilon_{N_1,a',r}\right) = \frac{\rho_{N_1,r}^{|a-a'|}\sigma_{N_1,r}^2}{\left(1 - \rho_{N_1,r}^2\right)}.$$

Parametizing movement

For each season, there are at most $n_R - 1$ parameters determining movement among regions given starting an the season in region r in either the sequential or simultaneous configurations. Movement parameters are estimated on a transformed scale via a link function $g(\cdot)$. If survival and movement are occur simultaneously, the parameters are estimated a log link function is used and if they are separable, an additive logit link function (like a multinomial regression) is used. On the transformed scale, the general model for the movement parameter from region r to r' in season i and year y for individuals of age a is a linear function of both random and environmental effects:

$$g(\mu_{r \to r',y,a,i}) = \theta_{r \to r',i} + \epsilon_{r \to r',y,a,i} + \sum_{k=1}^{n_E} \beta_{r \to r',a,i,k} E_{k,y}.$$

The random effects $\epsilon_{r\rightarrow r',y,a,i}$ are season-, and(or) region-to-region-specific and modeled most generally as 2DAR1 random effects with age and(or) year where the covariance is

$$Cov\left(\epsilon_{r\rightarrow r',y,a,i}, \epsilon_{r\rightarrow r',y',a',i}\right) = \frac{\rho^{|a-a'|}_{r\rightarrow r',\text{age},i}\rho^{|y-y'|}_{r\rightarrow r',\text{year},i}\sigma^2_{r\rightarrow r',i}}{\left(1-\rho^2_{r\rightarrow r',\text{age},i}\right)\left(1-\rho^2_{r\rightarrow r',\text{year},i}\right)}$$

similar to how WHAM models variation in survival, natural mortality, and selectivity. Effects of covariate E_k can be age-, season-, and(or) region-to-region-specific $\beta_{r\rightarrow r',a,i,k}$ and the same orthogonal polynomial options in the previous versions of WHAM for effects on recruitment and natural mortality are available.

There is currently no likelihood component for tagging data. Therefore, movement parameters would generally either need to be fixed or assumed to have some prior distribution, possibly based on external parameter estimates. We include prior distributions for the season and region-to-region specific (mean) movement parameters which are treated as random effects with the mean defined by the initial value of the fixed effect counterpart and standard deviation

$$\gamma_{r\rightarrow r',i} \sim \mathrm{N}\left(\theta_{r\rightarrow r',i}, \sigma^2_{r\rightarrow r',i}\right).$$

When priors are used, the movement is defined instead as

$$g(\mu_{r\rightarrow r',y,a,i}) = \gamma_{r\rightarrow r',i} + \epsilon_{r\rightarrow r',y,a,i} + \sum_{k=1}^{n_E}\beta_{r\rightarrow r',a,i,k}E_{k,y}$$

Natural mortality

Natural mortality options have been expanded in WHAM. When not estimated, (mean) mortality rates may be stock-, region-, and age-specific. When random effects are used, the same 2DAR1 structure with age and year as described by Stock and Miller (2021) can be configured for a given stock and region. Any environmental covariate effects can be stock-, region-, and age-specific. So the general model for natural mortality is

$$\log M_{y,a,r} = \theta_{M,r} + \epsilon_{M,r,y,a} + \sum_{k=1}^{n_E}\beta_{M,r,a,k}E_{k,y}.$$

The general covariance structure for random effects are modeled most generally as 2DAR1 random effect with age and(or) year where the covariance is

$$Cov\left(\epsilon_{M,y,a,r}, \epsilon_{M,y',a',r}\right) = \frac{\rho^{|a-a'|}_{M,\text{age},r}\rho^{|y-y'|}_{M,\text{year},r}\sigma^2_{M,r}}{\left(1-\rho^2_{M,\text{age},r}\right)\left(1-\rho^2_{M,\text{year},r}\right)}.$$

Catch observations

The log-normal distributional assumption for aggregate catch observations is the same as Stock and Miller (2021), but the predicted catch is now a function of catch from each stock starting the year in each region. For a given stock and age, the numbers captured in each fleet over the year are

$$\widehat{\mathbf{N}}_{H,s,y,a} = \mathbf{H}'_{s,y,a}\mathbf{N}_{O,s,y,a}$$

The predicted numbers caught be each fleet across stocks is

$$\widehat{\mathbf{N}}_{H,y,a} = \sum_{s=1}^{n_S} \widehat{\mathbf{N}}_{H,s,y,a}$$

and the predicted aggregate catch at age a is

$$\widehat{\mathbf{C}}_{y,a} = \operatorname{diag}\left(\mathbf{c}_{y,a}\right)\widehat{\mathbf{N}}_{H,y,a}$$

where $\mathbf{c}_{y,a}$ is the vector of mean individual weight at age a for each fleet and the aggregate catch by fleet is

$$\widehat{\mathbf{C}}_{y} = \sum_{a=1}^{A} \widehat{\mathbf{C}}_{y,a}$$

The log-aggregate catch observations for fleet f are normally distributed

$$\log C_{y,f} \sim \mathrm{N}\left(\log \widehat{C}_{y,f}, \sigma^2_{y,f}\right).$$

The predicted numbers caught for each fleet f (row f of $\widehat{\mathbf{N}}_{H,y,a}$) are used to make predicted age composition observations as described by Stock and Miller (2021). Since then, three additional likelihood options for age composition observations have been added: a logistic-normal with AR(1) correlation structure (Francis 2014), the alternative Dirichlet-multinomial parameterization described by Thorson et al. (2017), and the multivariate Tweedie (Thorson et al. 2023).

Index observations

For index m occurring in region r_m at fraction of the year t_m, the predicted abundance at t_m in region r_m is

$$\widehat{N}_{s,y,a,m} = \mathbf{O}_{s,y,a,r_m}(t_m)'\mathbf{N}_{O,s,y,a}$$

where $\mathbf{O}_{s,y,a,r_m}(t_m)$, the r_m column of the upper-left submatrix of Eq. 4, are the probabilities of surviving and occurring in region r_m at time t_m given being alive in each region at the start of the year. The predicted index at age is

$$\widehat{I}_{m,y,a} = q_{m,y}\text{sel}_{m,y,a}w_{m,y,a}\sum_{s=1}^{n_S}\widehat{N}_{s,y,a,m}$$

where $q_{m,y}$ is the catchability of the index in year y, $\text{sel}_{m,y,a}$ is the selectivity and $w_{m,y,a}$ is the average weight of individuals at age a if the index is quantified in biomass and $w_{m,y,a} = 1$ if the index is quantified in numbers. Predicted age composition observations are functions of $\widehat{I}_{m,y,a}$ as described by Stock and Miller (2021) and the likelihood options are the same as those for catch explained above.

Catchability of the index can also be treated as functions of normal random effects and(or) environmental covariate effects

$$log\frac{q_{m,y} - l_m}{u_m - q_{m,y}} = \theta_{q,m} + \varepsilon_{q,m,y} + \sum_{k=1}^{n_E}\beta_{q,m,k}E_{k,y}$$

where u_m and l_m are the upper and lower bounds of catchability for index m (defaults are 0 and 1000) and the general covariance structure for the annual random effects is AR1

$$Cov\left(\epsilon_{q,m,y}, \epsilon_{q,m,y'}\right) = \frac{\rho_{q,m}^{|y-y'|}\sigma_{q,m}^2}{1-\rho_{q,m}^2}.$$

Weight and Maturity at age

Weight and maturity at age are treated similarly to Stock and Miller (2021). Annual weight at age matrices for each fleet are used to calculate total catch and the weight at age is applied to catch numbers at age for any stocks caught by the fleet. Similarly, when indices and(or) associated age composition observations are measured in biomass, the weight at age matrices for the index are applied to predicted numbers at age of all stocks observed by the survey. Unique weight at age and maturity at age matrices are allowed for each stock to calculate spawning stock biomass.

Reference points

Currently a single F reference point $\widetilde{F}$ is estimated across stocks and regions and F by fleet and age is $\widetilde{F}_{f,a} = \widetilde{F}\text{sel}_{f,a}$. Selectivity is determined as before when there are multiple fleets where $\text{sel}_{f,a}$ is determined by averaging F at age over a user-defined set of years

$$\text{sel}_{a,f} = \frac{\overline{F}_{a,f}}{\max_a \sum_{f=1}^{n_F}\overline{F}_{a,f}}$$

The equilibrium spawning stock biomass per recruit for stock s in region r_s is defined as

$$\phi_s(\widetilde{F}) = \sum_{a=1}^{A} \widetilde{\mathbf{O}}_{s,a,r_s,\cdot}\mathbf{O}_{s,a,\cdot,r_s}(t_s) w_{s,a} m_{s,a} \tag{6}$$

where $w_{s,a}$ and $m_{s,a}$ are the mean individual weight and probability of maturity at age a, $\widetilde{\mathbf{O}}_{s,a}$ are as described in Eq. 5, and $\mathbf{O}_{s,a}(t_s)$ is the $n_R \times n_R$ upper-left sub-matrix of eq. 3 with the probabilities of surviving and occurring in each region r' at age $a + t_s$ given starting in region r at age a. The further subscripts $r_s, \cdot$ and $\cdot, r_s$ indictate row or column r_s, respectively. Using these rows and columns is required because of the assumption that spawning and recruitment only occur in region r_s.

The equilibrium spawning biomass per recruit (eq. 6) is conditional on the region of recruitment r_s. The equilibrium recruitment in each region $\widetilde{\mathbf{N}}_{s,1}$, depends on the stock dynamics. This version of WHAM currently only allows complete spawning region fidelity so that a stock only spawns and recruits in a single region. In this case, $\widetilde{\mathbf{N}}_{s,1}$ will be positive in the spawning region (r_s) and zero elsewhere. Similarly, the row r_s of $\mathbf{O}_s$ will be zero off of the diagonal. The matrices of probabilities of surviving and occurring in each region, $\widetilde{\mathbf{O}}_{s,a}$ and $\mathbf{O}_{s,a}(\delta_s)$, are functions of the fishing mortality rates for fleets in each region $\widetilde{F}_{f,a}$.

The matrix equilibrium yield per recruit as a function of $\widetilde{F}$ is calculated as

$$\widetilde{Y}_s(\widetilde{F}) = \sum_{a=1}^{A} \widetilde{\mathbf{O}}_{s,a,r_s,\cdot}\mathbf{H}_{s,a}\mathbf{c}_{s,a} \tag{7}$$

where $\mathbf{c}_a$ is the vector of mean individual weight at age for each fleet, and $\mathbf{H}_{s,a}$ is the submatrix of the probabilities of being captured in each fleet over the interval from a to $a + 1$, defined in eq. 1.

As in previous versions of WHAM package, “static’’ reference points, typically meant to be defined for prevailing conditions, average all of the inputs to the spawning biomass and yield per recruit calculations over the user-specified years (e.g., last 5 years of the model). This same averaging is also applied to possibly time-varying movement parameters.

For $X\%$ SPR-based reference points, we use a Newton method and iterate

$$\log \widetilde{F}^{(i)} = \log \widetilde{F}^{(i-1)} - \frac{g\left(\log \widetilde{F}^{(i-1)}\right)}{g'\left(\log \widetilde{F}^{(i-1)}\right)} \tag{8}$$

where $g(\log F)$ is the difference between the weighted sums of spawning biomass per recruit at F and $X\%$

of unfished spawning biomass per recruit across stocks:

$$g(\log F) = \sum_{s=1}^{n_s} \lambda_s \left[\phi_s \left(F = e^{\log F} \right) - \frac{X}{100} \phi_s \left(F = 0 \right) \right].$$

where $\phi_s\left(F = 0\right)$ is the equilibrium unfished spawning biomass per recruit. $g'(\log F)$ is the derivative of g with respect to $\log F$, and the weights to use for each stock λ_s can be specified by the user or relative to the average of recruitment for each stock over the same years the user defines to calculate "static'' equilibrium spawning biomass and yield.

When a Beverton-Holt or Ricker stock recruit relationship is assumed, an analogous Newton method is used to find $\log F$ that maximizes yield for MSY-based reference points. which are also a functions of the equilibrium yield per recruit (7) and equilibrium recruitment. The function $g(\log F)$ in Eq. 8 is the first derivative of the yield curve with respect to $\log F$.

Projections

The projection options are generally the same as those for previous versions of WHAM. When there is movement of any stocks, the user has the option to project and use any random effects for time-varying movement or use the average over user specified years, analogous to how natural mortality can be treated in the projection period. The projection of any environmental covariates has been revised to better include error in the estimated latent covariate in any effects on the population in projection years.

Application to black sea bass

Prior to its 2023 peer-reviewed assessment, the NEUS black sea bass stock was assessed using the Age-Structured Assessment Program (ASAP) model (Legault and Restrepo 1999), a single-stock and -region statistical catch-at-age model that estimates all model parameters as fixed effects. Northern and southern components of the NEUS black sea bass stock ascribed to regions divided by the Hudson Canyon were separately modeled in ASAP (reference map figure). Results from the separate ASAP models were combined for a unit-stock assessment. The ASAP-based assessments exhibited strong retrospective patterns (Mohn 1999), and exploring alternative modeling approaches for the northern and southern stock components has been a high priority for management.

Leading up to the 2023 peer-reviewed assessment, a working group (hereafter referred to as "working group") composed of scientists from federal, state, and academic institutions determined an optimal data and model configuration for the black sea bass stock using the multi-stock and multi-region extension of WHAM described above (NEFSC 2023). This assessment included the spatial features and investigated inclusion of hypothesized environmental drivers that were prioritized research recommendations from previous black sea bass assessments.

Below we describe the assumptions and configuration of the assessment model as determined by the working group as well as the alternative assumptions for recruitment and natural mortality in the models we fit to evaluate alternative hypotheses of bottom temperature effects on black sea bass.

Basic structure

The first year being modeled for the population is 1989 and the fishery and index data used in the model span from 1989 to 2021. The north and south stock components are modeled as separate populations that spawn and recruit in respective regions. We have observations for each of four total fishing fleets, where two fishing fleets (Recreational and Commercial) operate in each region.

There are 11 seasonal intervals within each calendar year: five monthly time intervals from Jan 1 to May 31, a spawning season from June 1 to July 31, and five monthly intervals from August 1 to December 31. The southern stock component is assumed to never move to the northern region. For the northern component, a proportion $\mu_{\mathrm{N}\to\mathrm{S}}$ can move to the southern region each month during the last five months of the year, but no movement is allows from the south to the north during this period (Figure 1). During the first four intervals of the year a proportion $\mu_{\mathrm{S}\to\mathrm{N}}$ the northern component individuals in the south can move back to the north, but no movement from the north to south is allowed during this period. In the fifth interval (May), all northern component individuals remaining in the south are assumed to move back to the north for the subsequent spawning period. Survival and movement occur sequentially in each interval and each of the two movement proportions are assumed constant across intervals, ages, and years.

The two monthly movement matrices are

$$\boldsymbol{\mu}_1 = \begin{bmatrix} 1 - \mu_{\mathrm{N}\to\mathrm{S}} & \mu_{\mathrm{N}\to\mathrm{S}} \\ 0 & 1 \end{bmatrix}$$

for the portion of the year after spawning and

$$\boldsymbol{\mu}_2 = \begin{bmatrix} 1 & 0 \\ \mu_{\mathrm{S}\to\mathrm{N}} & 1 - \mu_{\mathrm{S}\to\mathrm{N}} \end{bmatrix}$$

for the portion of the year before spawning. As noted in the description of the general WHAM model, tagging data are not yet allowed. However, the working group also fit a Stock Synthesis model (Methot and Wetzel 2013) which provided estimated movement rate parameters and standard errors that were used to configure the priors for WHAM (see Supplementary Materials).

With the movement configuration, the northern origin fish (ages 2+) can occur in the southern region on January 1. Estimating initial numbers at age as separate parameters can be challenging even in single-stock models, but for black sea bass the available data cannot distinguish the proportion of northern and southern component fish at each age in the southern region in the initial year of the model. Therefore, we used the simplifying equilibrium assumption described above where there are two parameters estimated for each stock component: an initial recruitment and an equilibrium fully-selected F that determines the abundance at age in each region for each stock component.

For the northern population abundance at age 1 on January 1 (recruitment) is only allowed in the northern region, but given the monthly movement described above, older individuals that previously recruited in the northern region may occur in the southern region on January 1. Therefore, a model with survival random effects will model the transitions (survival/movement) of abundances at age of northern origin fish in each region. All of the initial runs assumed variance parameters for these random effects to be the same for northern origin fish occurring in both regions on January 1. The base model assumes very small variance for the transitions of northern fish in the southern region, which is approximately the same as the deterministic transition assumptions of a statistical catch at age model. We also allow 2DAR1 correlation for recruitment and survival for both the northern and southern components. Unique variance and correlation parameters for the recruitment and survival random effects are estimated for the northern and southern components.

Uncertainty recreational CPA index observations

The estimated coefficients of variation (CVs) provided by the analyses to generate the recreational catch per angler (recreational CPA) index ranged between 0.02 and 0.06 which the working group felt did not capture the true observation uncertainty in the index with regard to its relationship to stock abundance. In many of the initial runs as well as the base model we allowed a scalar multiple of the standard deviation of the log aggregate index to be estimated for these indices in the northern and southern regions. Models that successfully estimated these scalars indicated standard deviations for these surveys to be approximately 5 times the input value and this value was fixed in many preliminary runs to avoid dealing with convergence problems. However, the base model successfully estimated these scalars. The model estimates are negligibly affected by estimating these scalars, but we felt estimating these parameters allowed uncertainty in model output to be more properly conveyed.

Index and Catch age composition observations

The working group investigated many alternative assumptions for the probability models and selectivity models for the 8 different sets of age composition observations to reduce residual patterns and retrospective patterns. These analyses resulted in use of selectivity random effects for the northern fleet and indices and logistic-normal likelihoods for 6 sets of of age composition observations and Dirichlet-multinomial likelihoods for one index and one fleet in the northern region (Table S1).

Bottom Temperature effects

All model fits also include bottom temperature observations for the northern and southern regions from 1963 to 2021 and estimated standard errors ranging between 0.03 and 0.09 degrees Celsius (NEFSC 2023). We retained the assumption from the peer-reviewed assessment that treated the latent bottom temperature covariates in each region as AR1 processes.

We fit 14 models with alternative assumptions about the effects of bottom temperature covariates, ranging from no effects to effects on both regions for either recruitment or natural mortality at age 1 (Table 1). These analyses derive from the hypothesis that bottom temperature affects overwinter survival of fish where the fish turn from age 0 to age 1 on January 1 (Miller et al. 2016a). This temperature may be a proxy for temperature prior to January 1 and affect survival during the end of the pre-recruit phase or natural mortality in the early part of of the year after becoming age 1. Furthermore, we have no direct observations of age 1 individuals from surveys until the spring season each year. Therefore, we fit models with effects of temperature on recruitment or natural mortality at age 1.

It is standard practice to treat annual recruitment as time-varying deviations from a mean model and all models here treat recruitment deviations as AR1 random effects. However, Miller et al. (2018) showed how inferences of temperature effects on growth or maturity parameters can be very different whether the compared models with and without the effect also include random effects representing residual temporal variation in parameters. Therefore, we also explored whether including temporal random effects on age 1 natural mortality affected inferences on corresponding temperature effects. Initially, we included random effects on age 1 natural mortality for both the northern and southern stock components, but estimates of these random effects and corresponding variance for the southern component converged to 0 so these were not included in models presented here.

We assume the covariate in year y affects recruitment in the same years because the covariate observations are from months January to March. The fish are technically already 1 year old, but there are no observations of these individuals until later in the year except possibly in fishery catches which are accumulated over the whole year. Expected log-recruitment for a given stock is a linear function of bottom temperature

$$E\left(\log N_{y,1}|x_y\right) = \mu_R + \beta_R x_y. \tag{9}$$

Similarly, expected log-natural morality as a function of bottom temperature is

$$E\left(\log M_{y,1}|x_y\right) = \mu_{M,1} + \beta_M x_y \tag{10}$$

Because age 1 fish for the northern component can exist in both regions after January 1, natural mortality is acting in both regions for this stock. For models with covariate and/or annual random effects for age 1 fish we assume them only in the northern regions for the northern component. The corresponding random effects are

$$\log N_{y,1} = E\left(\log N_{y,1}|x_y\right) + \epsilon_{y,1} \tag{11}$$

and

$$\log M_{y,1} = E\left(\log M_{y,1}|x_y\right) + \epsilon_{M,y}. \tag{12}$$

The constant or mean log-natural mortality rate is assumed to be $\mu_{M,a} = \log(0.4)$ for all ages as recommended by the working group. Because the bottom temperature anomalies and random effects are centered at 0, mean log-natural mortality at age 1 over the time series should be approximately equal to $\mu_{M,1}$ for models that include those effects.

Model fitting, diagnostics, and projections

We used a development version (commit fb8b089) of the WHAM package prior to the release of version 2.0 for all results. All code for fitting models and generating results can be found at github.com/timjmiller/wham_bsb_paper.

We examined retrospective patterns for all models by fitting corresponding models where the terminal year is reduced sequentially by one year (peel) for seven years. Therefore, there are eight fits of each model with the time series reduced by zero to seven years. We calculated Mohn's ρ for SSB, and average F at ages 6 and 7. Absolute values of Mohn's ρ near 0 imply no pattern in estimation of these quantities as the time-series is sequentially extended.

As in Miller et al. (2016b), we also assessed the consistency of the AIC-based model selection over retrospective peels to guard against previously noted changes in perception of covariate effects on recruitment with increased length of the time series of observations (Myers 1998). This retrospective examination was also recommended by Brooks (2024).

We performed a jitter analysis of the base model M_0 and the best fitting model to investigate whether a local mimimum of the negative log-likelihood surface was obtained by the optimization. We used the jitter_wham function in the WHAM package which by default simulates starting values from a multivariate normal distribution with mean and covariance defined by the MLEs and estimated covariance matrix from the fitted model. See the Supplementary Materials for more details.

For the best performing model, we also performed so-called simulation self-tests where new observations were simulated conditional on all estimated fixed and random effects and the same model configuration was fit to each of the simulated data sets. We estimated median relative bias of SSB across these simulations. See the Supplementary Materials for more details.

To illustrate projections with environmental effects we projected the best black sea bass model under three alternative scenarios where the AR1 time-series model for bottom temperature continues into the projection years, where we project with bottom temperature being the average of the most recent 5 years, and where bottom temperature increases following a predictions from a simple linear regression of the estimated bottom temperature anomalies over time.

Results

We found the best model of bottom temperature covariate effects included the effect only on the recruitment of the northern stock (Table 2). However, the difference in AIC for the model that also included effects on recruitment for the southern component suggested some evidence for this hypothesis as well (Table 3).

Across retrospective peels where the terminal year of data was sequentially reduced, the ranking for the best model was consistent. However, when the terminal year was reduced 6 or more years, there was more evidence for further effects of temperature on recruitment for the southern component and for temporal variation in natural mortality at age 1 (Table 3).

The retrospective model fits did not indicate any evidence of patterns for northern or southern component SSB (all Mohn's $\rho \approx -0.03$) or fishing mortality (all Mohn's $\rho \approx 0.03$ and -0.04 for average F at ages 6 and 7 in north and south regions, respectively) for any of the models (Table 4).

Bottom temperature effects

The posterior estimate of the bottom temperature covariate match the observations well because of the high precision of the observations and anomalies in the north and south region appear highly correlated (Figure 3). Because the temperature anomalies are treated as latent variables, when effects on recruitment are included, other data components in the model can affect the estimated anomalies (e.g., Miller et al. 2018), but in this case the estimates are altered negligibly during the years where recruitment is estimated (Figure S5).

Estimated effects of bottom temperature on recruitment for either the northern or southern component were stable over the retrospective peels and differed negligibly whether effects for each component were estimated in isolation or together (Table 5). Estimates of residual variability in northern component recruitment, as measured by the conditional or marginal standard deviation of the recruitment random effects, increased slightly with the number of peeled years. However, the ratio of standard deviations of models with and without temperature effects was stable with about a 20% reduction in residual standard deviation when temperature effects were included.

Although evidence for temperature effects on age 1 natural mortality was weak, it is notable that the sign of the estimated effect for the northern stock component differed depending on whether random effects on age 1 natural mortality were also included ($\widehat{\beta}_R = -1$ for M_6 or M_{13}) with the negative effect estimated with these random effects (M_{13}).

Stock size, fishing

For the best performing model M_1, estimates of SSB Stock size is also increasing for the southern component, just not as quickly as the northern component. (plot of SSB time series for each component).

Figure 5

Figure S4 Annual estimates of SSB and F varied little among the 14 fitted models.

plot of prior/posterior for movement rate.

plot of average F by fleet,region.

Sectivity random effects (Figure 7)

Estimates of effect size, sd, correlation for each peel (Table **??**

The residual variation in the standard deviation of recruitment random effects is reduced because the expected recruitment (Eq. 9) is a function of the covariate. This effect is included in the proposed base model (Figure 4).

plot of northern component predicted recruitment vs. time with color by bottom temperature

Reference points

Projections

Projections of bottom temperature and recruitment and CVs (Figure 6)

Uncertainty in both is much lower during the data years than the projection years.

Uncertainty in BT RE propagates into both expected recruitment and estimated random effect for recruitment, but the latter also includes uncertainty due to the residual variability in recruitment.

Discussion

General Model aspects

WHAM provides a comprehensive treatment of environmental covariates and their effects on populations using state-space methods (Maunder 2024). This framework accounts for the magnitude of differing uncertainties in observations and stochastic population dynamics processes. This version 2.0 extends these inferences to movement rates for multi-region models.

Future developments

An obvious limitation to WHAM is the inability to include tagging observations of any type. Such observations are critical to estimation of movement parameters (e.g., Goethel et al. 2019), but also can inform mortality rate parameters (Hampton 1991). It is well known that natural mortality is seldom estimated in assessment models because the observed data often provide little information to distinguish natural mortality from other assessment model parameters (Lee et al. 2011; Clark 2022). Estimation of natural mortality may be even more challenging within state-space assessment models with their greater flexibility from inclusion of time-varying random effects. For example, we fixed the mean natural mortality for age 1 fish and Cadigan (2016) and Stock et al. (2021) also estimated natural mortality deviations. Therefore allowing tagging observations in WHAM should be a high priority even for models with a single stock and region.

The work by Correa et al. (2023) on incorporating length information and modeling growth within WHAM has not yet been merged into the multi-stock version 2.0. Growth and movement would be challenging.

Black sea bass

In our investigation of bottom temperature effects on recruitment and natural mortality and time-varying random effects on natural mortality at age 1, we found only including effects on recruitment for the northern stock component to be the best model with respect to AIC. This is the same configuration configuration accepted during the assessment peer-review process and it is the model currently used for management (NEFSC 2023).

Although not relevant to the best performing model, the effect of bottom temperature on age 1 M would be expected to be opposite of that for recruitment because lower M with higher temperature would produce higher recruitment. This expected effect was estimated only when random effects on age 1 M were also included in the model. This seems to provide further support to including random effects when examining covariate effects on population parameters as demonstrated by Miller et al. (2018) for effects on growth parameters.

AIC suggested some weight for models with temperature effects on recruitment for the southern component and random effects on M at age 1. This might suggest making inferences on the population by using an ensemble of these and weighting by AIC (Burnham and Anderson 2002). However, the estimates of assessment outputs relevant for management (SSB, F) were similar among the models and weighted estimates would differ very little from the estimates with the lowest AIC. [but what about reference points?]

Temperature effects

BSB in the NEUS is at the northern extent of its range. hence the range extension to the north with increased temperature. The evidence for temperature effects on recruitment was strong only for the northern component which is the component of the stock at the limit of the species' range. Opposite effects of temperature on recruitment or population size would be expected for species in the same general area that are at the southern extent of their range (Gabriel 1992). For example, higher recruitment of the Southern New England-Mid-Atlantic stock of yellowtail flounder is correlated with more cold water persistence into summer fall on the Northeast US shelf Miller et al. (2016b).

Self Tests

Simulation self tests performed by Stock and Miller (2021) simulated process errors and observation errors and their simulations showed little bias in estimated assessment output such as SSB. Li et al. (2024) used the same type of simulations and found what?.

Here we conditioned on the estimated process errors for black sea bass. This conditional approach has been suggested as appropriate for tactical management where we are interested in inferences assuming our estimation of the population and fishing history from the original data is the truth Cadigan et al. (2024). We found some bias in SSB estimation for the black sea bass application (negatively for the northern stock), using the default model. We also found instability in the estimation of the observation variance parameters for the aggregate indices such that they often were estimated at the lower bound of 0. However, we found that the magnitude of bias was largely influenced by the large uncertainty estimated in some of the age composition observations assumed to have a logistic-normal distribution. When using the logistic-normal likelihood for management, we recommend inspecting the size of the estimated (marginal) standard deviation of the logistic normal model when self-test bias is non-negligible. We also recommend investigating the multiplicative transformation for the logistic normal rather than the additive transformation which is currently the only option in WHAM (Cadigan 2016).

?Selectivity RE are only on index age comp in the north which may be why bias is larger there?

? We found REML provided less biased estimation of SSB and recruitment which are functions of random effects. Whether REML should be the default approach for estimating these quantities from state-space stock assessment models requires further investigation. For example, improvement in bias may be negligible when data contain low observation error and/or there are few fixed effects parameters. ? larger variance estimates allows greater spread of random effects estimates. Important for conditional self-test where estimated RE are of primary importance (Recruitment and SSB). When simulating RE and refitting, the sign of differences between estimates and true values can be random across simulations. Probably more important with more fixed effects and less informative data

Including tagging data in WHAM would also be helpful for BSB because we are using the same data to estimate movement outside of the model as we are using to estimate the other parameters in WHAM.

Conclusions

WHAM version 2.0 extends the existing R package to allow multiple stocks and discrete spatial regions. It allows autocorrelated random effects and environmental covariate effects on movement rates. Estimates of movement rates from auxiliary studies can be used to construct prior distributions for movement rates in lieu of integrated likelihoods for tagging data. Version 2.0 also allows seasonal treatment of different fishing fleets and movement of individual stocks, and internal estimation of SPR- and MSY-based reference points accounting for seasonal spatial dynamics including movement and mortality and any environmental covariate effects.

We applied this extended version to investigate alternative hypotheses about effects of bottom temperature on recruitment and age 1 natural mortality for black sea bass. Our analyses indicate evidence for effects of bottom temperature on recruitment for the northern component represents was stronger than other models that included effects on age 1 mortality and/or corresponding effects on the southern stock component.

Future WHAM development should prioritize including tagging data to inform stock assessment parameter estimation and merging in the version created by Correa et al. (2023) to allow modeling of growth and inclusion of length and length-at-age composition observations.

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Appendix A

Table A1: Definition of terms.

i	Seasonal time interval
δ_i	Length of seasonal time interval i
a	Age class
y	Year
A	Last age class (“plus group”)
r	Region
f	Fishing fleet
n_F	Number of fishing fleets
s	Stock
n_R	Number of regions
$\mathbf{P}_{y,a,i}$	Probability transition matrix for year y, age a, and season i
$\mathbf{O}_{y,a,i}$	submatrix of $\mathbf{P}_{y,a,i}$ of probabilities of surviving and occuring in each region for year y, age a, and season i
$\mathbf{H}_{y,a,i}$	submatrix of $\mathbf{P}_{y,a,i}$ of probabilities of being captured in each fishing fleet for year y, age a, and season i
$\mathbf{I}_H$	n_f x n_f identity matrix
m	Index observation
$O_{y,a,i}(r,r')$	For year y, age a and season i, the probability of surviving and occurring in region r' given beginning the interval alive in region r
$H_{y,a,i}(r,f)$	For year y, age a and season i, the probability of being captured in fleet f given beginning the interval alive in region r
$S_{y,a,i}$	For year y, age a and season i, the probability of surviving the interval (1 region model)
$F_{y,a,i,f}$	Fishing mortality rate for fleet f in year y at age a in seasonal interval i
$M_{y,a}$	Natural mortality rate in year y at age a (single region)
$M_{y,a,r}$	Natural mortality rate in region r and year y at age a
$Z_{y,a,i}$	Total mortality rate in year y at age a in seasonal interval i (single region)
$Z_{y,a,i,r}$	Total mortality rate in region r and year y at age a in seasonal interval i
$\mathbf{S}_{y,a,i}$	matrix of of probabilities of surviving in each region over the interval for season i, year y, age a

Table A1: (Continued)

$\boldsymbol{\mu}_{y,a,i}$	matrix of of probabilities of moving or staying in each region at the end of season i in year y and age a
$\mu_{r\to r',y,a,i}$	For year y, age a and seasonal interval i, either the probability of moving at the end of the interval or instantanteous rate of movement from region r to region r'
r_f	region where fleet f operates
$\mathbf{N}_{y,a}$	Column vector of abundances by region at age a in year y
$\mathbf{A}_{y,a,i}$	instantaneous rate matrix for seasonal interval i, year y, and age a
$a_{y,a,i,r}$	For year y, age a and seasonal interval i, the hazard or negative sum of the instantaneous rates of mortality and movement from the state corresonding to being alive in region r
$\mathbf{P}_{y,a}(\delta_1,\ldots,\delta_K)$	Probability transition matrix for year y and age a over seasonal intervals $\delta_1,\ldots,\delta_K$
K	Number of seasons in the annual time step
t_s	fraction of the annual time step when spawning occurs for stock s
$\delta_{s,j}$	fraction of the annual time step between t_s and the end of season $j-1$
t_m	fraction of the annual time step when index m observers the population
$\delta_{m,j}$	fraction of the annual time step between t_m and the end of season $j-1$
$\mathbf{N}_{y,a}$	Abundance at age a in year y in each of the living and mortality states on January 1
$\mathbf{N}_{O,y,a}$	Abundance at age a in year y alive in each region on January 1
$N_{y,a,r}$	Abundance at age a in year y alive in region r on January 1
r_s	region where stock s spawns and recruits
$\mathrm{SSB}_{s,y}$	Spawning stock biomass for stock s in year y
$\varepsilon_{y,a,r}$	Random error for abundance at age a in year y in region r
$w_{s,y,a}$	mean individual weight for stock s at age a in year y
$\mathrm{mat}_{s,y,a}$	proportion mature at age a in year y for stock s
$\mathbf{O}_{s,y,a,r_s}(t_s)$	Probabilities of surviving and occurring in region r_s at time t_s given being alive in each region at the start of the year
$\boldsymbol{\varepsilon}_{y,a}$	vector of random errors for abundance alive in each region on January 1 of year y at age a
$\sigma_{N,r}$	standard deviation parameter for abundance at age random effects in region r
$\rho_{N,\mathrm{age},r}$	first order auto-regressive correlation parameter across age for abundance at age random effects in region r
$\rho_{N,\mathrm{year},r}$	first order auto-regressive correlation parameter across year for abundance at age random effects in region r

Table A1: (Continued)

$\text{sel}_{1,a,f}$	selectivity at age a for fleet f in the first year
$F_{1,a,f}$	fishing mortality rate at age a for fleet f in the first year
$\widetilde{F}_{a,f}$	equilibrium fishing mortality rate at age a for fleet f
$\mathbf{O}_a$	proportion surviving the year at age j and occuring in each region (columns) given alive on January 1 in each region (rows)
$\widetilde{\mathbf{O}}_a$	equilibrium proportions alive in each region at age a (columns) given recruitment in each region (rows)
$\mathbf{N}_{O,1,r}$	vector of abundance by age in region r in the first year
$\theta_{N_1,r}$	mean parameter for initial numbers at age random effects in the first year for region r
$\boldsymbol{\varepsilon}_{N_1,r}$	vector of random effects by age for initial numbers at age in the first year for region r
$\sigma_{N_1,r}$	standard deviation parameter for initial numbers at age random effects in the first year for region r
$\rho_{N_1,r}$	first order auto-regressive correlation parameter for initial numbers at age random effects in the first year for region r
$\mu_{r\to r',y,a,i}$	movement from region r to region r' in seasonal interval i and year y at age a
$g(\mu_{r\to r',y,a,i})$	link function for movement $\mu_{r\to r',y,a,i}$
$\theta_{r\to r',i}$	mean parameter across age and year for movement from region r to region r' in seasonal interval i
$\epsilon_{r\to r',y,a,i}$	random effect parameter for movement from region r to region r' in seasonal interval i and year y at age a
n_E	number of environmental covariates
$\beta_{r\to r',a,i,k}$	effect of environmental covariate k on movement from region r to r' at age a in seasonal interval i
$E_{k,y}$	latent environmetal covariate k affecting the population in year y
$\sigma_{r\to r',i}$	standard deviation parameter for movement random effects from region r to r' in seasonal interval i
$\rho_{r\to r',\text{age},i}$	first order auto-regressive correlation parameter across age for movement random effects from region r to r' in seasonal interval i
$\rho_{r\to r',\text{year},i}$	first order auto-regressive correlation parameter across year for movement random effects from region r to r' in seasonal interval i

Table A1: (Continued)

$\gamma_{r \to r',i}$	random effect for link-transformed mean movement from region r to r' in seasonal interval i when a prior distribution is assumed
$\sigma_{r \to r',i}$	standard deviation parameter for prior distribution of $\gamma_{r \to r',i}$
$M_{y,a,r}$	natural mortality rate for age a in year y in region r
$\theta_{M,r}$	mean parameter across age and year for nutural mortality in region r
$\epsilon_{M,r,y,a}$	random effect parameter for natural mortality in region r and year y at age a
$\beta_{M,r,a,k}$	effect of environmental covariate k on natural mortality in region r at age a
$\sigma_{M,r}$	standard deviation parameter for natural mortality random effects in region r
$\rho_{M,\text{age},r}$	first order auto-regressive correlation parameter across age for natural mortality random effects in region r
$\rho_{M,\text{year},r}$	first order auto-regressive correlation parameter across year for natural mortality random effects in region r
$\widehat{\mathbf{N}}_{H,s,y,a}$	vector of predicted numbers of stock s at age a in year y captured by each fleet
$\widehat{\mathbf{N}}_{H,y,a}$	vector of predicted numbers at age a in year y captured by each fleet across all stocks
$\widehat{\mathbf{C}}_{y,a}$	vector of predicted biomass captured at age a in year y by each fleet across all stocks
$\mathbf{c}_{y,a}$	vector of mean individual weight at age a in year y for each fleet
$\widehat{\mathbf{C}}_{y}$	vector of predicted aggregate catch for each fleet in year y
$C_{y,f}$	observed aggregate catch for fleet f in year y
$\widehat{C}_{y,f}$	predicted aggregate catch for fleet f in year y
$\sigma_{y,f}$	standard deviation of observed log-aggregate catch for fleet f in year y
$\widehat{N}_{s,y,a,m}$	predicted abundance at t_m in region r_m
$\mathbf{O}_{s,y,a,r_m}(t_m)$	the probabilities of surviving and occurring in region r_m at time t_m given being alive in each region at the start of the year which is the r_m column of the upper-left submatrix of Eq. 4
$\widehat{I}_{m,y,a}$	Predicted relative abundance index for survey d in year y at age a
$q_{m,y}$	catchability of index m in year y
$\text{sel}_{m,y,a}$	selectivity of index m at age a in year y
$w_{m,y,a}$	average weight of individuals at age a for index m if the index is quantified in biomass, otherwise it is unity
u_m	upper bound for index m catchability
l_m	lower bound for index m catchability
$\theta_{q,m}$	mean index m catchability parameter

Table A1: (Continued)

$\varepsilon_{q,m,y}$	index m catchability random effect in year y
$\beta_{q,m,k}$	effect of environmental covariate k on index m catchability
$\sigma_{q,r}$	standard deviation parameter for index m catchability random effects
$\rho_{q,m}$	first order auto-regressive correlation parameter across year for index m catchability random effects

Figures

	Jan Feb Mar Apr May	Jun Jul	Aug Sep Oct Nov Dec
Northern Component	Monthly survival and movement south	Survival and spawning	Monthly survival and movement north
Southern Component	Monthly survival	Survival and spawning	Monthly survival

Figure 1: Diagram of intervals within the year and configuation of the dynamics of each component of the BSB population.

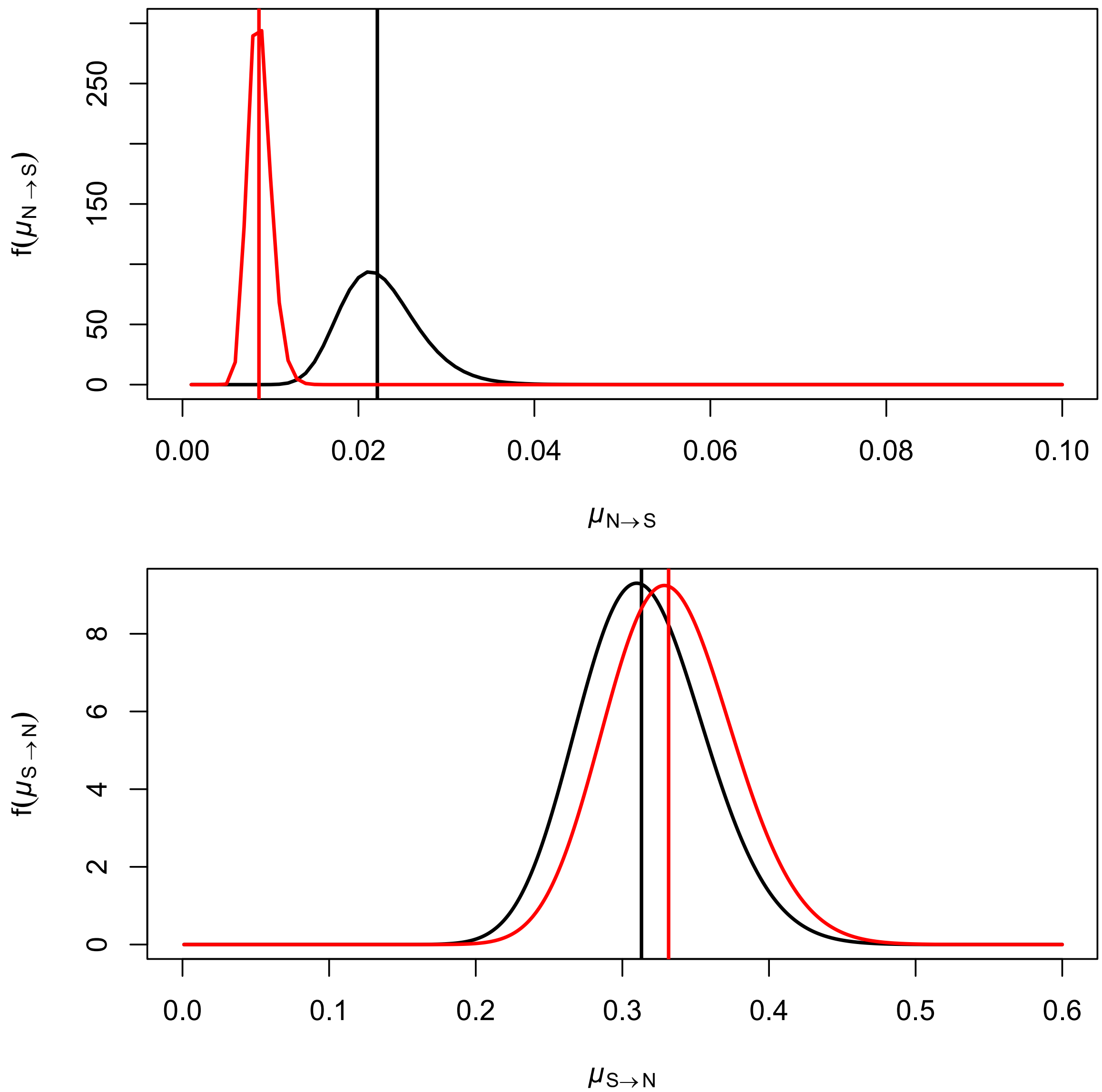

Figure 2: Prior (black) and posterior (red) distributions of movement of northern component stock from north to south (top) and south to north (bottom).

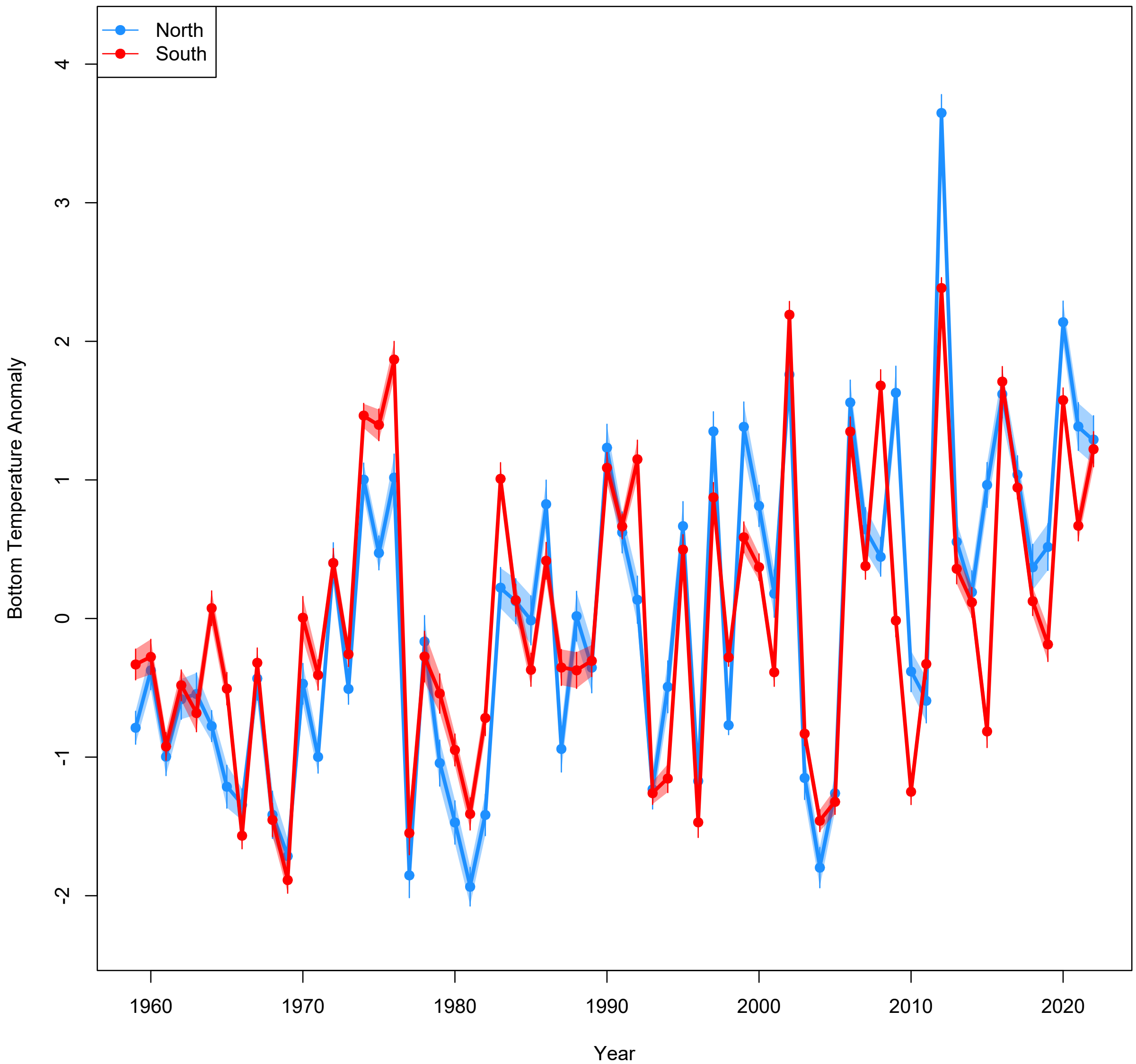

Figure 3: Observations and 95% confidence intervals (points with vertical lines) and posterior estimates (lines) with 95% confidence intervals (polygons) of bottom temperature anomalies in the north and south regions from model M_0.

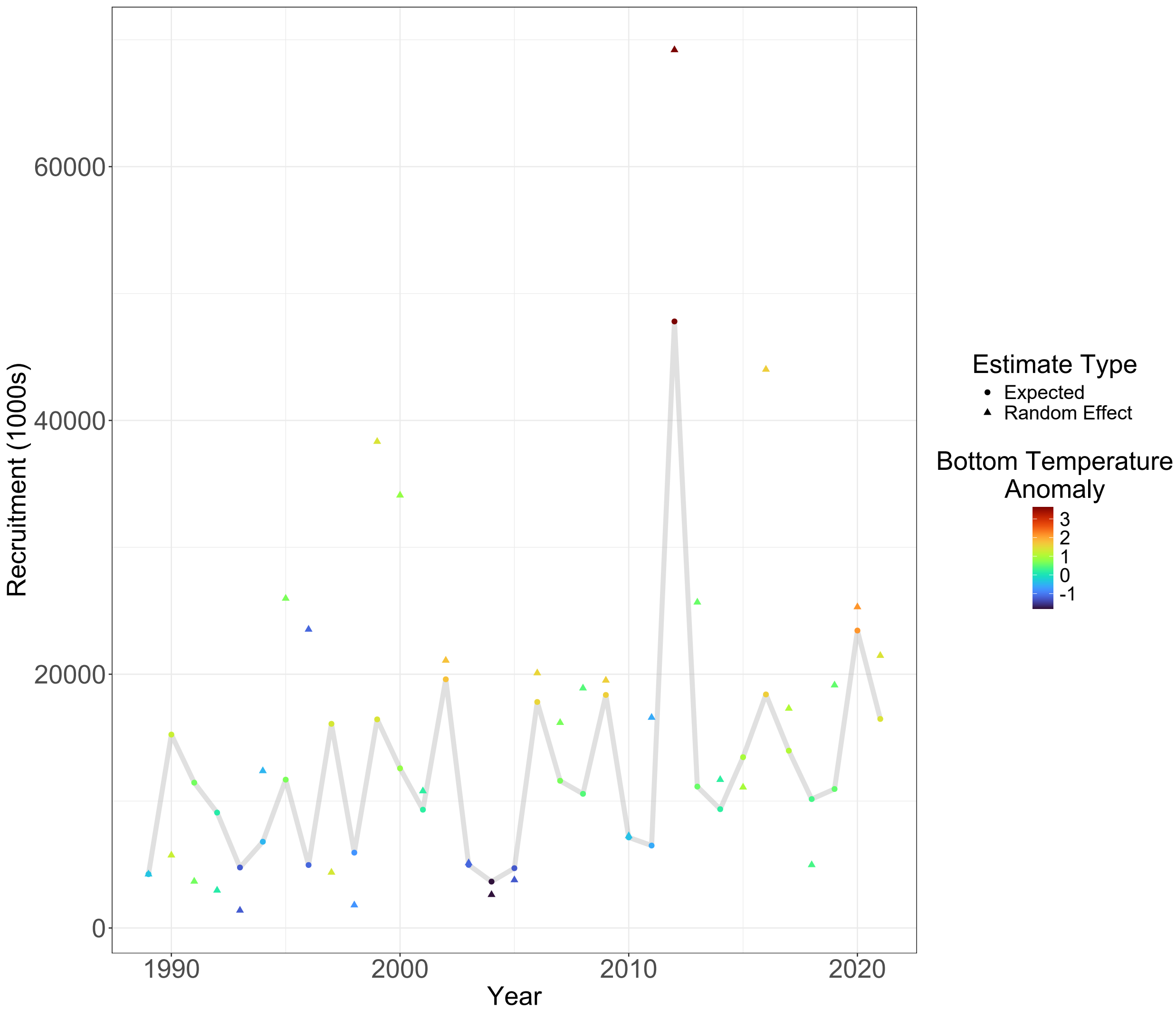

Figure 4: Expected and Posterior Emperical Bayes estimates of annual recruitment for the northern stock component. Color defined by the corresponding annual bottom temperature anomaly.

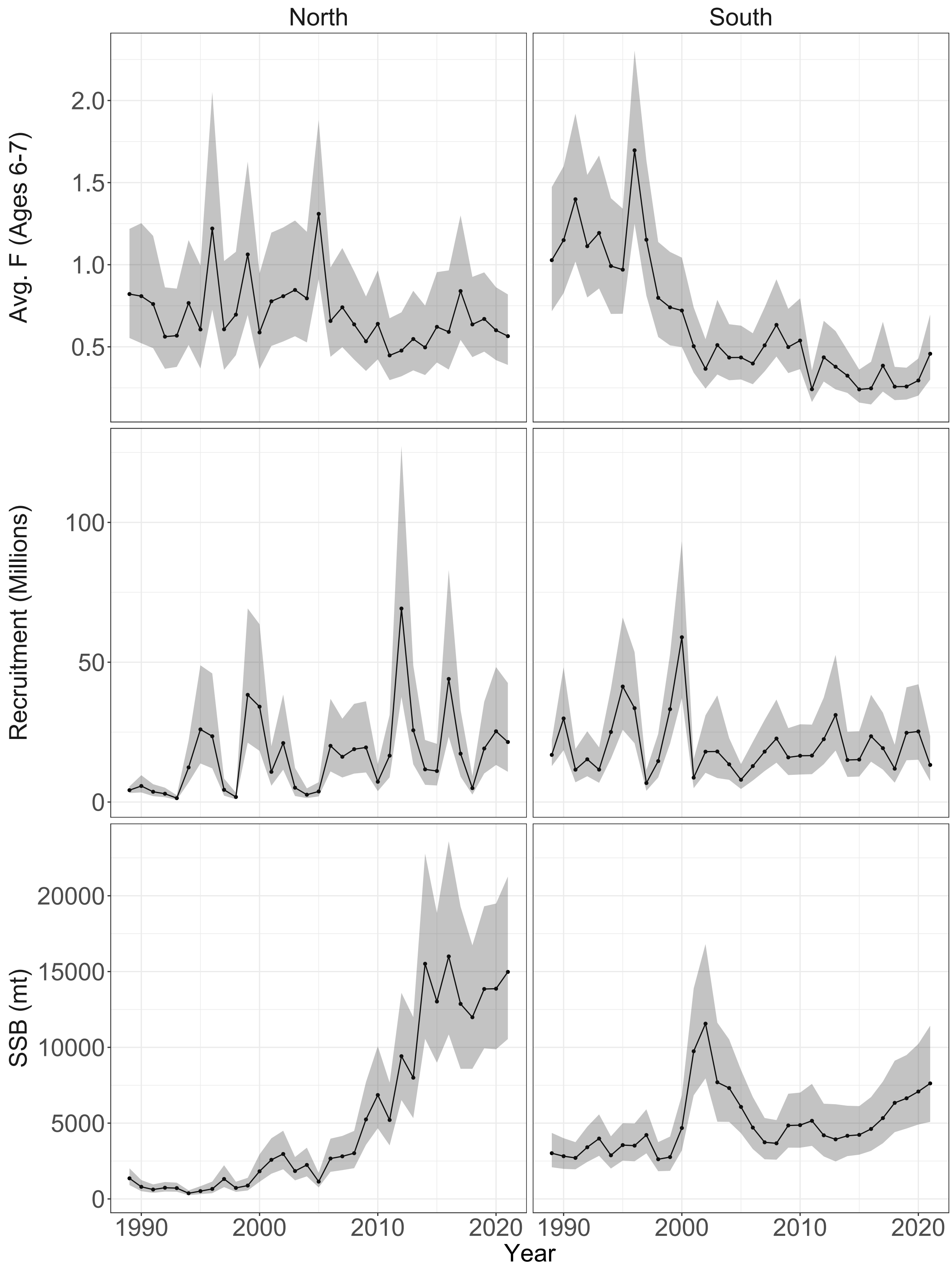

Figure 5: Annual estimates of SSB, average F (ages 6-7), and recruitment from model M_1. Polygons represent 95% confidence intervals.

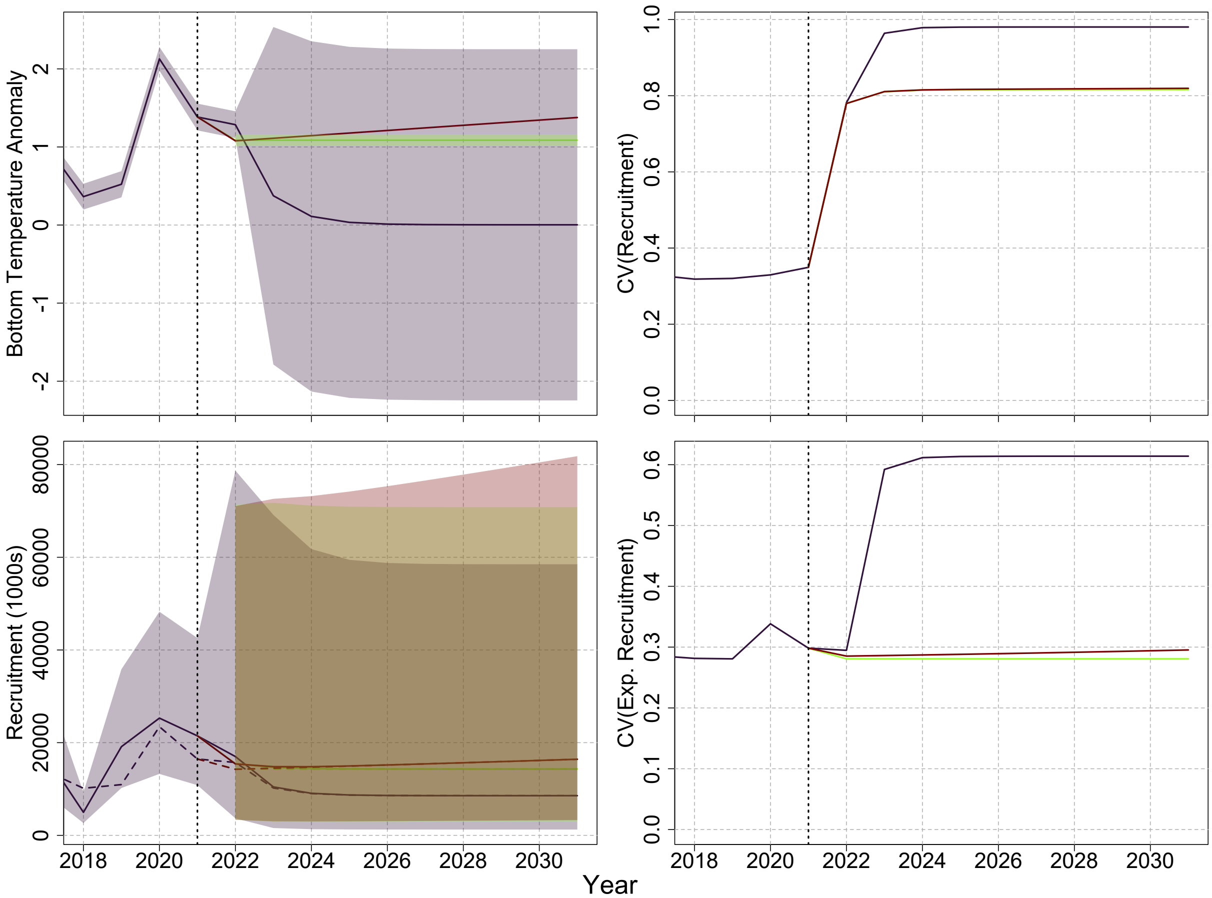

Figure 6: Estimates of bottom temperature, recruitment, and expected recruitment, and coefficients of variation for the latter two from model M_1 assuming alternative bottom temperature scenarios described in the text. Polygons represent 95% confidence intervals.

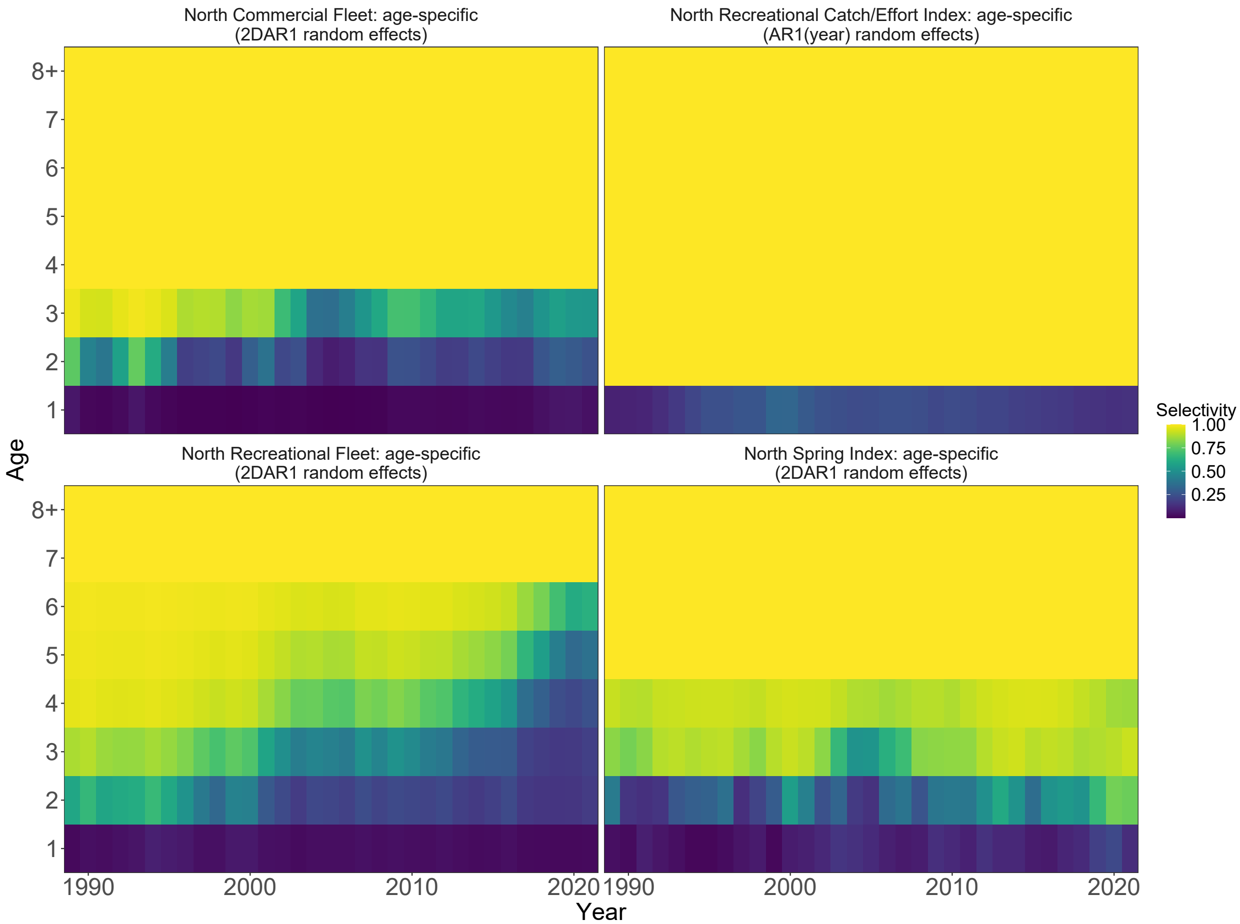

Figure 7: Time and age-varying selectivty for fleets and indices in the northern region with autoregressive random effects.

Table 1: Assumptions for temperature effects and random effects for age 1 natural mortality for each model.

	Temperature Effect		
Model	North	South	M at age 1 random effects
M_0	–	–	none
M_1	Recruitment	–	none
M_2	–	Recruitment	none
M_3	Recruitment	Recruitment	none
M_4	M at age 1	–	none
M_5	–	M at age 1	none
M_6	M at age 1	M at age 1	none
M_7	–	–	time-varying
M_8	Recruitment	–	time-varying
M_9	–	Recruitment	time-varying
M_{10}	Recruitment	Recruitment	time-varying
M_{11}	M at age 1	–	time-varying
M_{12}	–	M at age 1	time-varying
M_{13}	M at age 1	M at age 1	time-varying

Tables

Table 2: Difference between AIC and the lowest AIC for each model by retrospective peel.

	Peel							
Model	0	1	2	3	4	5	6	7
M_0	11.83	11.39	10.41	10.05	9.86	9.41	8.47	8.22
M_1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_2	12.63	12.03	11.41	11.06	10.91	10.34	9.20	9.22
M_3	0.80	0.64	1.00	1.01	1.05	0.93	0.73	1.00
M_4	13.81	13.35	12.26	11.82	11.71	11.18	10.08	9.85
M_5	13.25	12.55	11.68	11.21	11.07	10.41	9.86	9.71
M_6	15.22	14.51	13.52	12.97	12.91	12.17	11.46	11.33
M_7	14.32	13.75	12.17	11.30	11.43	10.55	9.71	9.42
M_8	2.25	2.10	1.47	0.96	1.29	0.91	0.98	0.99
M_9	15.12	14.39	13.17	12.31	12.48	11.49	10.44	10.43
M_{10}	3.05	2.74	2.47	1.97	2.34	1.84	1.71	1.99
M_{11}	16.29	15.74	14.17	13.30	13.43	12.55	11.68	11.39
M_{12}	15.73	14.91	13.43	12.46	12.64	11.55	11.10	10.92
M_{13}	17.70	16.91	15.43	14.46	14.64	13.55	13.07	12.88

Table 3: Model AIC weights for each retrospective peel.

	Peel							
Model	0	1	2	3	4	5	6	7
M_0	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
M_1	0.45	0.43	0.42	0.38	0.41	0.37	0.36	0.38
M_2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_3	0.30	0.31	0.25	0.23	0.24	0.23	0.25	0.23
M_4	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_8	0.15	0.15	0.20	0.24	0.21	0.24	0.22	0.23
M_9	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_{10}	0.10	0.11	0.12	0.14	0.13	0.15	0.15	0.14
M_{11}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_{12}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_{13}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 4: Mohn's ρ for SSB, and average F at ages 6 and 7 in northern and southern regions.

	SSB		Average F	
Model	North	South	North	South
M_0	-0.040	-0.023	0.041	-0.048
M_1	-0.040	-0.023	0.041	-0.048
M_2	-0.040	-0.024	0.041	-0.047
M_3	-0.040	-0.024	0.041	-0.047
M_4	-0.041	-0.022	0.042	-0.048
M_5	-0.041	-0.023	0.042	-0.048
M_6	-0.042	-0.023	0.042	-0.048
M_7	-0.042	-0.022	0.043	-0.048
M_8	-0.044	-0.023	0.044	-0.048
M_9	-0.042	-0.024	0.043	-0.048
M_{10}	-0.044	-0.024	0.044	-0.047
M_{11}	-0.041	-0.022	0.042	-0.048
M_{12}	-0.042	-0.023	0.043	-0.048
M_{13}	-0.041	-0.023	0.042	-0.048

Table 5: Estimates of temperature effects on recruitment and variance and autocorrelation parameters for recruitment for northern (N) and southern (S) components for models with no effects (M_0), effects on specific components (M_1 and M_2) or both components simultaneously (M_3) from the full model (Peel 0) and each retrospective peel.

	Peel							
Parameter	0	1	2	3	4	5	6	7
M_1 $\widehat{\beta}_{R,N}$	0.474	0.480	0.485	0.476	0.464	0.468	0.439	0.445
M_2 $\widehat{\beta}_{R,S}$	0.099	0.105	0.094	0.095	0.092	0.096	0.099	0.091
M_3 $\widehat{\beta}_{R,N}$	0.474	0.480	0.485	0.476	0.464	0.468	0.439	0.445
M_3 $\widehat{\beta}_{R,S}$	0.099	0.105	0.094	0.095	0.092	0.096	0.099	0.091
M_0 Conditional $\widehat{\sigma}_{R,N}$	0.925	0.953	0.978	0.988	0.978	1.010	0.981	1.007
M_1 Conditional $\widehat{\sigma}_{R,N}$	0.730	0.752	0.780	0.786	0.775	0.801	0.785	0.800
M_0 $\widehat{\rho}_{R,N}$	0.362	0.375	0.385	0.405	0.424	0.432	0.427	0.431
M_1 $\widehat{\rho}_{R,N}$	0.296	0.307	0.334	0.373	0.394	0.406	0.428	0.429
M_0 Marginal $\widehat{\sigma}_{R,N}$	0.992	1.028	1.060	1.080	1.081	1.120	1.084	1.117
M_1 Marginal $\widehat{\sigma}_{R,N}$	0.764	0.791	0.827	0.848	0.843	0.877	0.869	0.885

Supplemental Materials

Deriving the prior distribution for movement parameters

The working group fit a Stock Synthesis model (Methot and Wetzel 2013) that included tagging data with 2 seasons (6 months each) and 2 regions where a proportion μ_1^* of the northern component moves to the south in one season and some proportion $\mu_{2\to 1}^*$ move back to the south in the second season (NEFSC 2023). The seasonal movement matrices for each season are

$$\boldsymbol{\mu}_1^* = \begin{bmatrix} 1-\mu_{1\to 2}^* & \mu_{1\to 2}^* \\ 0 & 1 \end{bmatrix}$$

and

$$\boldsymbol{\mu}_2 = \begin{bmatrix} 1 & 0 \\ \mu_{2\to 1}^* & 1-\mu_{2\to 1}^* \end{bmatrix}.$$

To obtain estimates of movement proportions for the monthly intervals in the WHAM model, the half-year movement matrices were converted to monthly movement matrices by taking the root z_k of $\boldsymbol{\mu}_k^*$ which are defined by the number of months of movement for each season (5 and 4, respectively). The roots of the matrices are calculated using an eigen decomposition of the matrices

$$\boldsymbol{\mu}_k = (\boldsymbol{\mu}_k^*)^{z_k} = \mathbf{V}_k \mathbf{D}_k^{z_k} \mathbf{V}_k^{-1}$$

where $z_1 = 1/5$ for and $z_2 = 1/4$, and $\mathbf{V}_k$ and $\mathbf{D}_k$ are the matrix of eigenvectors (columnwise) and the diagonal matrix of corresponding eigenvalues of $\boldsymbol{\mu}_k^*$. The working group used a parametric bootstrap approach to determine an appropriate standard deviation for the prior distribution for the movement parameters. Stock Synthesis also estimates parameters on a transformed scale, but different from WHAM:

$$\mu_{r\to r'}^* = \frac{1}{1+2e^{-x_{r\to r'}}}$$

The estimated parameters and standard errors from the Stock Synthesis model were $x_{1\to 2} = -1.44$ and $x_{2\to 1} = 1.94$ and $SE(x_{1\to 2})) = 0.21$ and $SE(x_{2\to 1})) = 0.37$. The resulting in the estimated proportions were $\mu_{1\to 2}^* = 0.11$ and $\mu_{2\to 1}^* = 0.78$.

In WHAM, an additive logit transformation is used which is simply a logit transformation when there are only two regions:

$$\mu_{r \to r'} = \frac{1}{1 + e^{-y_{r \to r'}}}.$$

We simulated 1000 values from a normal distribution with mean and standard deviation defined by the parameter estimate and standard error $\tilde{x}_{r \to r',b} \sim N(x_{r \to r'}, SE(x_{r \to r'}))$ from the Stock Synthesis model. For each simulated value we constructed $\tilde{\boldsymbol{\mu}}^*_{r \to r',b}$, took the appropriate root and calculated inverse logit for $\tilde{y}_{r \to r',b}$. We calculated the mean and standard deviation of the values $y_{i,b}$. The mean values did not differ meaningfully from the transformation of the original estimates ($y_{1 \to 2} = -3.79$ and $y_{2 \to 1} = -0.79$) and the standard deviation was approximately 0.2 for both parameters.

Diagnostics

0.0.1 Jitter fits for model M_0

WHAM by default completes three newton steps after the stats::nlminb minimization function completes to reduce the gradient at the minimized NLL. However, this generally has negligible effects on model estimates and the NLL. To reduce computation time, we did not complete these newton steps when performing jitter fits of the model. Without the Newton steps, the maximum (absolute) gradient sizes are generally less than 0.01 for models that converge satisfactorily.

The 50 jitter fits demonstrated that a local minimum was obtained for the original fit of model M_0 (Figure S1). Some lower NLLs were obtained with unacceptable gradients, but a slightly lower NLL was found with a satisfactory gradient and with and invertible hessian. We therefore refit model M_0 and all remaining models using the better parameter estimates as initial values.

0.0.2 Jitter fits for model M_1

The 50 jitter fits gave no evidence of a better minimization of the NLL. Three lower NLLs were obtained, but with unacceptably large gradients (Figure S2). The largest differences in parameter estimates for these three jitters were for numbers at age and selectivity random effects variance and correlation parameters.

0.0.3 Self test for model M_1

Initial fits to simulated data from model M_1 showed estimation of the observation error standard deviation multiplier for the recreational catch-per angler indices in the north and south regions was unstable. Many of the fits to the simulated data produced implausible estimates at the 0 boundary for these parameters (very negative values on log-scale). Therefore, we completed self-tests with these parameters fixed at the true values.

For 7 of the the simulated data sets the model failed to optimize. The maximum absolute gradient was $< 10^{-6}$ for only 9 and $< 10^{-4}$ for 52 of the 93 successfully fitted models. The poor convergence appeared to be attributable to the estimation of the scalar for the standard errors of the log-transformed northern Recreational CPA index for which estimates tended to 0 for nearly all of the fits (< 0.01 for 83 fits). However, even across all fits including those with poor convergence, the SSB estimates appeared to be reliable (Figure S3).

0.0.4 One-step-ahead residuals for model M_1

One-step-ahead residuals can now be calculated for all index, catch, and environmental covariate observations using methods described by Thygesen et al. (2017) and Trijoulet et al. (2023).

Table S1: Configuration of age composition likelihoods, mean selectivity models, and selectivity random effects models for each age composition data component. For all logistic-normal likelihoods, any ages observed as zeros are treated as missing.

Data component	Age Composition Likelihood	Mean Selectivity model	Random effects Model
North commercial fleet	Dirichlet-Multinomial	age-specific (ages $>$ 3 fully selected)	AR1 correlation by age and year
North recreational fleet	Logistic-normal (Independent)	age-specific (ages $>$ 6 fully selected)	AR1 correlation by age and year
South commercial fleet	Logistic-normal (AR1 correlation)	logistic	None
South recreational fleet	Logistic-normal (AR1 correlation)	logistic	None
North recreational CPA index	Logistic-normal (Independent)	age-specific (ages $>$ 1 fully selected)	AR1 correlation by year
North VAST index	Dirichlet-Multinomial	age-specific (ages $>$ 4 fully selected)	AR1 correlation by age and year
South recreational CPA index	Logistic-normal (AR1 correlation)	age-specific (ages $>$ 2 fully selected)	None
South VAST index	Logistic-normal (AR1 correlation)	age-specific (ages $>$ 1 fully selected)	None

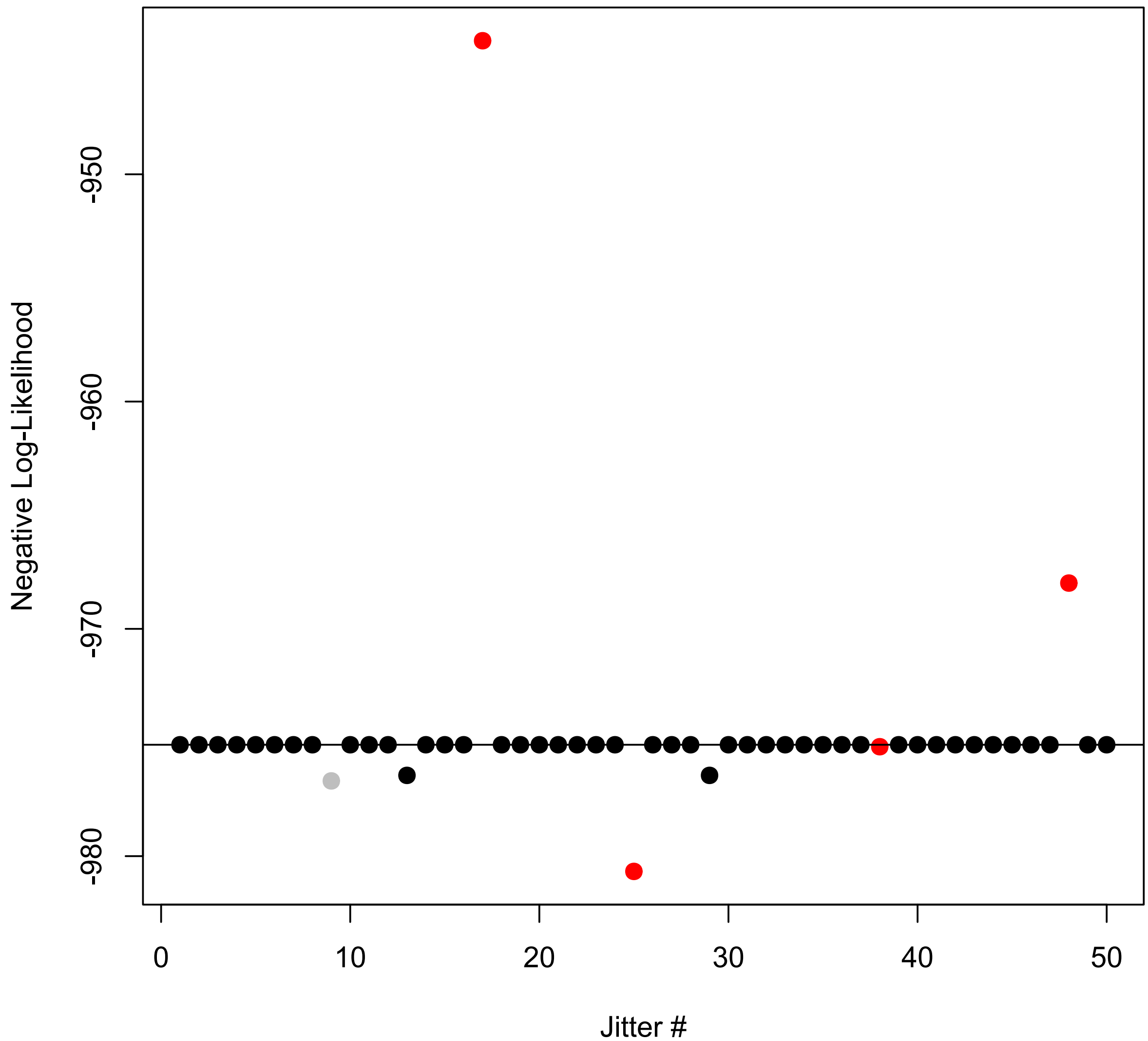

Figure S1: Minimized negative log-likelihood for 50 fits where minimization used initial parameter values jittered from those provided by an initial fit for model M_0. Black jitters had maximum absolute gradient values $< 10^{-10}$, grey jitters had values $> 10^{-10}$ and < 1, and red jitters had values > 1.

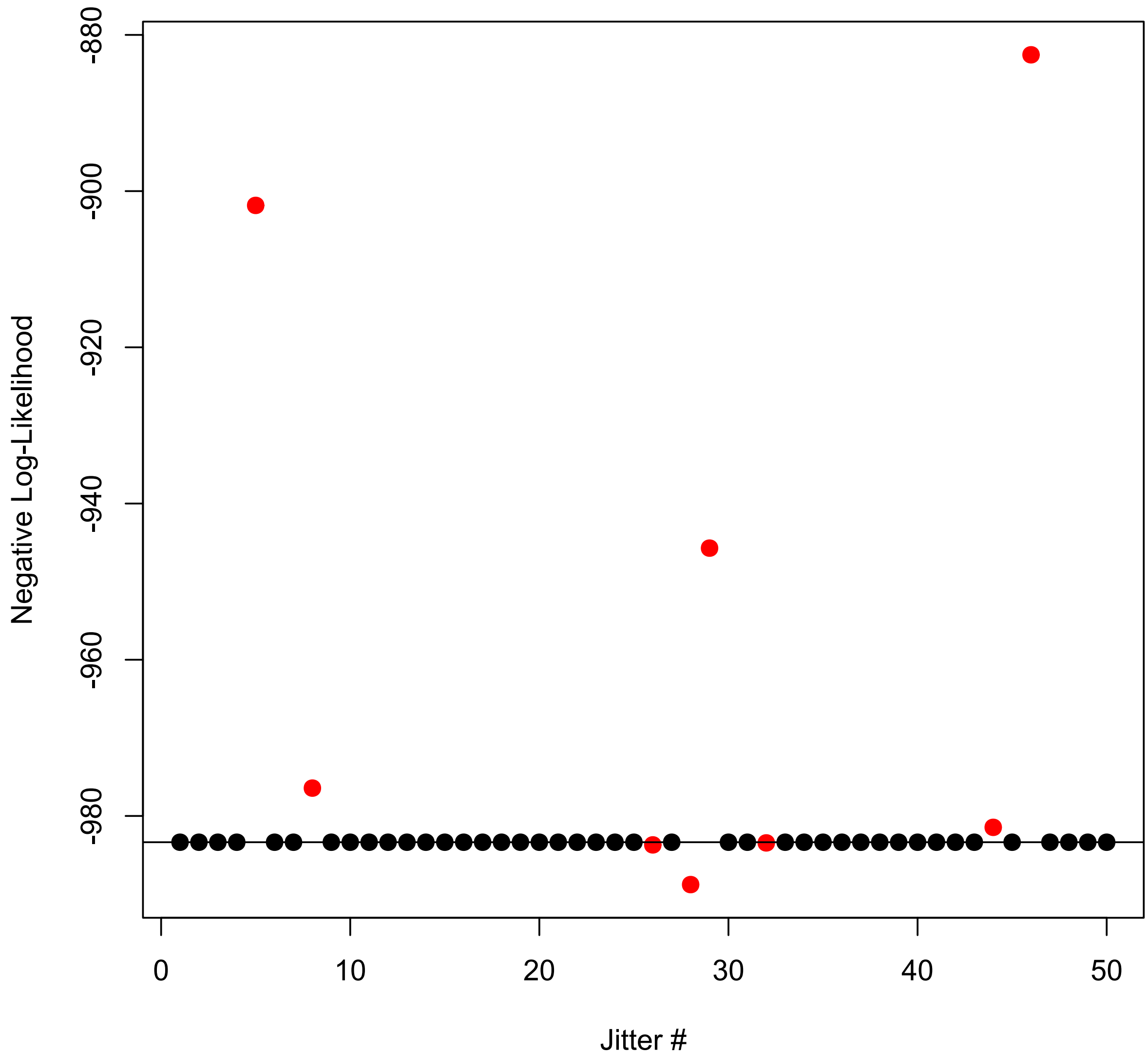

Figure S2: Minimized negative log-likelihood for 50 fits where minimization used initial parameter values jittered from those provided by an initial fit for model M_1. Fits with black dots had maximum absolute gradient value < 0.01 and fits with red dots had values > 10.

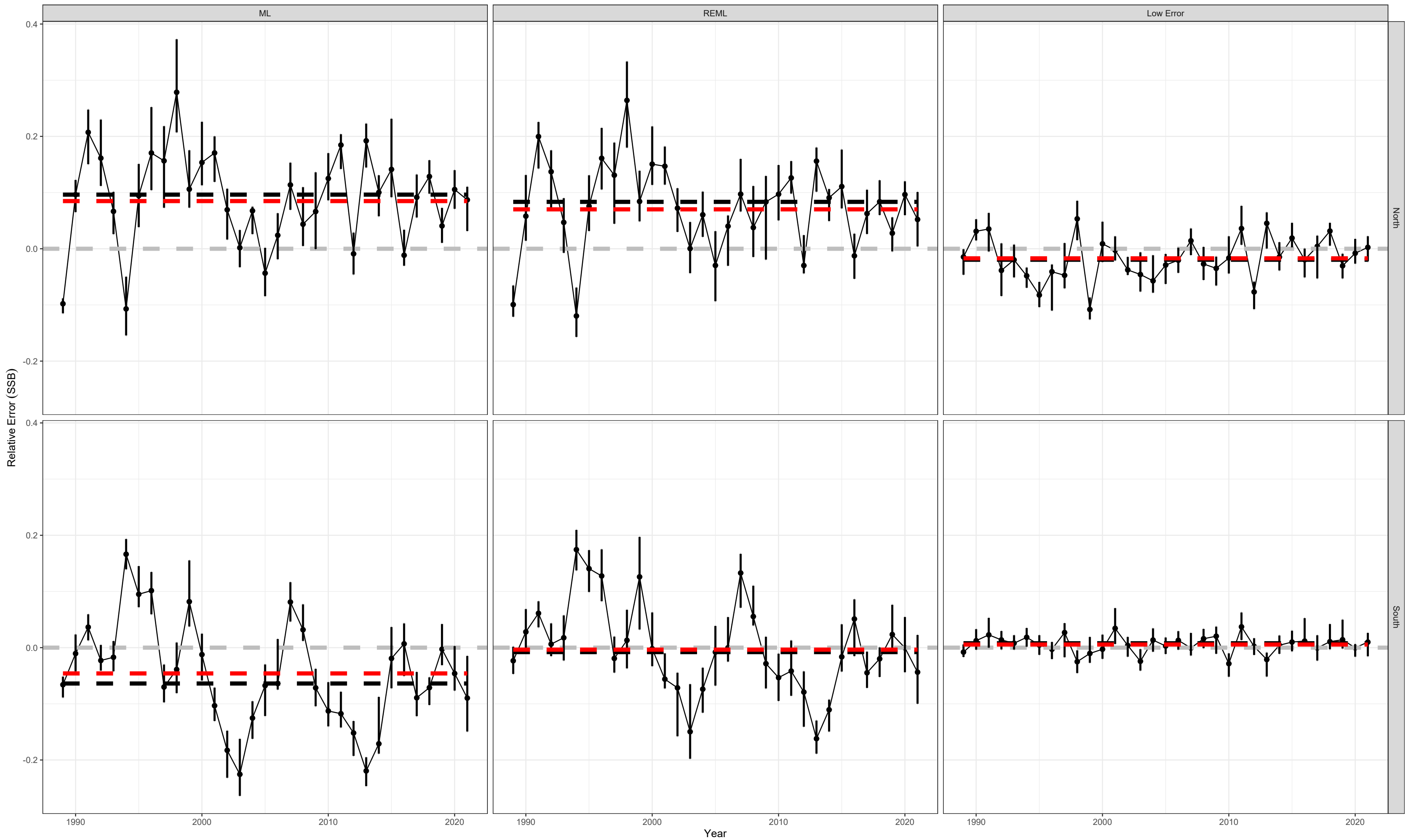

Figure S3: Median relative bias of SSB for the North and South stock components for estimation models where the observation variance of log-indices are fixed and estimation is by maximum marginal likelihood (ML) or Restricted Maximum Likelihood (REML) or where the standard deviation of logistic-normal age composition observations are assumed to be 0.1 (over sqrt(1000)) (Low Error). Black and Red dashed lines represent the median of the yeaerly medians and the median across all yearly relative errors, respectively.

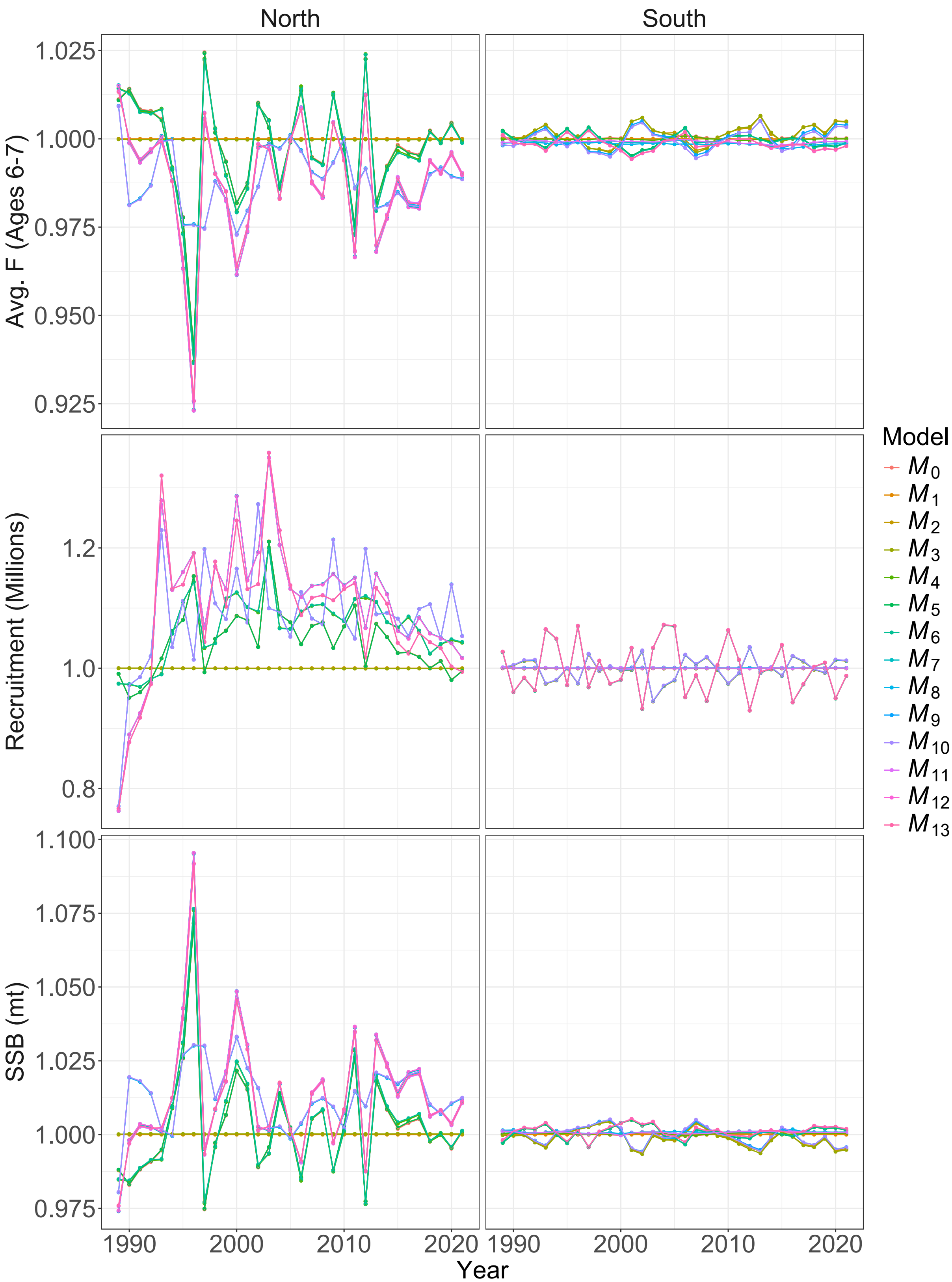

Figure S4: Estimates of SSB, F, and recruitment relative to those of the best performing model, M_1.

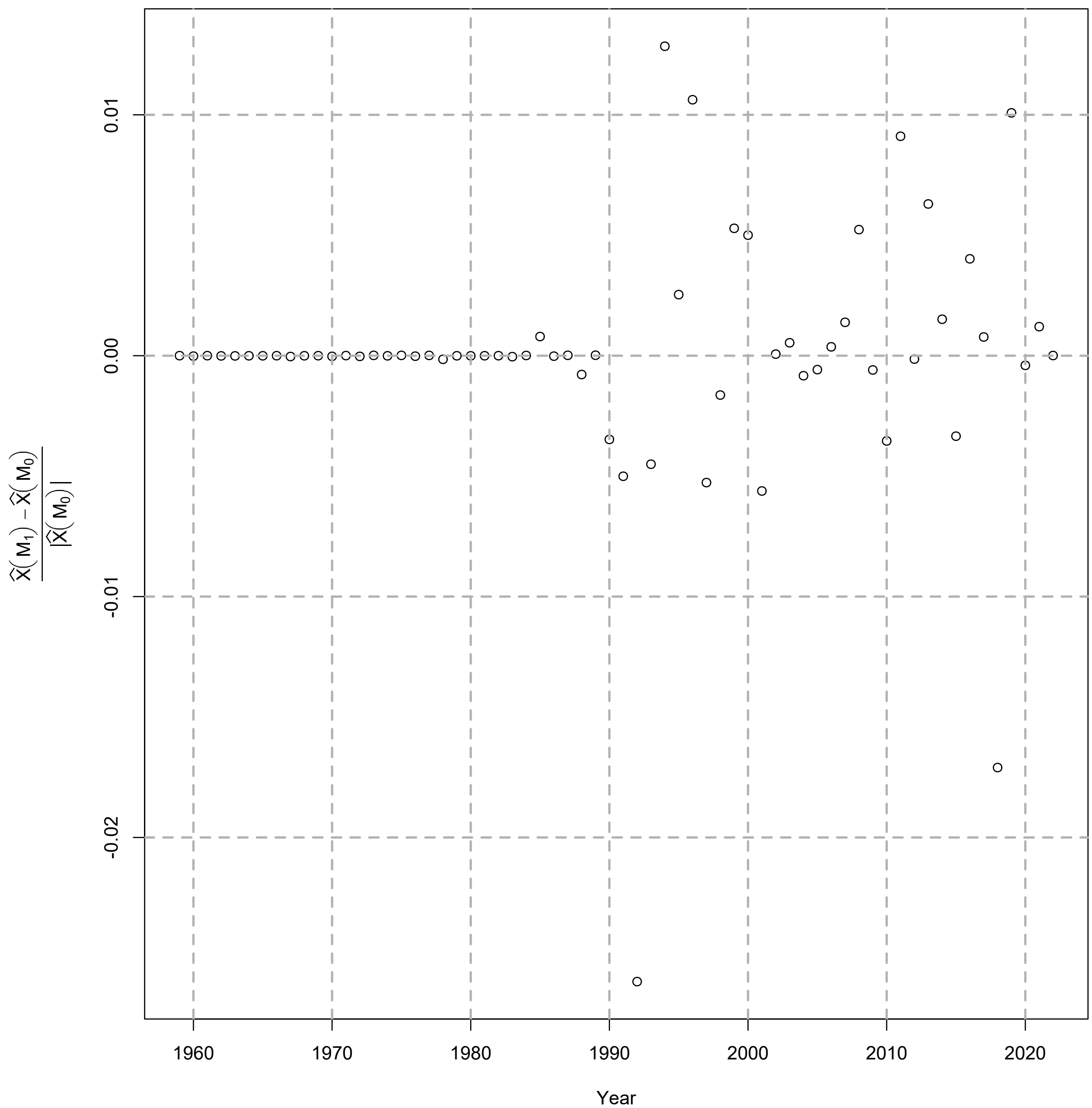

Figure S5: Relative differences in posterior estimates of northern region bottom temperature anomalies ($\widehat{X}$) from the null model without effects on recruitment (M_0) and with effects on the northern stock component (M_1).